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Dissertation

RETENTION OF CONDITIONED RESPONSES TO LIGHT FOLLOWING LESIONS TO THE STRIATE CORTEX

by

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CHAPTER I

INTRODUCTION

An animal conditioned to a visual intensive stimulus retains that response, at least to some degree, after ablation of the striate area of the cortex (1, 8, 9, 13, 19, 20, 21). It is presumed, therefore, that the cortex is not essentially involved in the learning and retention of conditioned responses to light intensity.

Marquis and Hilgard (9, pp. 6-7) are of the opinion that, "...after removal of the occipital lobe the conditioned response [to light intensity] is not mediated by a different mechanism functioning vicariously for the visual cortex", and further that, "...the cortex is not the essential neural mechanism for conditioning to light stimuli." The implication of the statement is that such learning involves subcortical pathways or "centers". Since the concept of neurological "centers" for psychological processes has been discarded, any effect that cortical lesions might have on an organism's responses is conceived of as the results of an interruption in a "relay network".

It is suggested that the striate cortex, or visual area, is but one of two or more relay systems involved in the retention of learned responses to light stimuli. Lesions to

the area may or may not lead to retention of learned responses to light stimuli depending both upon the nature of the responses and the stimuli involved. This would follow from the general position adopted since postulated psychological processes such as learning and discrimination are not conceived of as localized in any given part of the nervous system.

Where the avoidance conditioning technique has been used to estimate the postoperative retention of a learned response, positive results have been found. These studies have been restricted in at least two respects. First, the responses conditioned have been limited to the eyeblink and leg flexion. Second, the experiments have been carried out only on monkeys and dogs. Furthermore, the research in this area, with the exception of an experiment by Wing (20, 21) in which he measured the postoperative retention of a response to direction of light change, has been restricted to the use of a single light stimulus.

From the available data it is impossible to determine whether a differential response to two stimuli would survive removal of the striate area when the responses are acquired in a conditioning situation. In this regard, Marquis and Hilgard (8, p. 176) conclude their study on the effect of cortical ablation on a conditioned eyeblink by

noting that, "... it remains for further experimentation to determine whether or not a conditioned discrimination would be retained postoperatively."

I. THE PROBLEM

Statement of the Problem. This study was undertaken (a) to determine the effect of lesions of the striate area on the retention of a differential response to light stimuli; (b) to further investigate the findings of previous studies regarding the effects of partial lesions of the striate cortex on previously learned conditioned avoidance responses; (c) to determine whether or not findings based on research with dogs and monkeys apply to animals lower on the phylogenetic scale; (d) to learn whether or not lesions to the striate cortex produce the same effect on the retention of previously learned gross bodily responses as are produced on segmental responses.

The problem is of special significance in view of the findings of studies which have employed conventional discrimination techniques in studying the role of the striate cortex. These investigations (2, 3, 5, 7, 16) have found that ablation of the striate area results in amnesia for the problems presumably learned on the basis of intensive visual stimuli. The animals used in these studies, however, were able to relearn the discrimination in approximately

the same number of trials initially required.

Morgan (14, p. 472) writes concerning this situation, "The mystery is why there is a difference between conditioning and discrimination." This study does not intend to solve the "mystery" but the information gained should serve to limit the possible sources of explanation.

CHAPTER II

REVIEW OF THE LITERATURE

Relatively few conditioning studies have been carried out in order to ascertain the relationship of the striate cortex to the acquisition and retention of habits based on light stimulation.

Marquis and Hilgard (8) conditioned the eyeblink response in four dogs to a flash of light. A puff of air on the cornea served as the unconditioned stimulus. The conditioned response when established prior to the ablation of the striate area was retained after operation without additional training. The test showing retention was carried out five days after operation. The only change in the response was a slight increase in latency.

In another experiment using monkeys, Marquis and Hilgard (9) found similar thought less convincing results. One of three monkeys trained in a conditioned eyeblink showed retention of the conditioned response postoperatively. The animals displaying retention received the following treatment: He was conditioned in the eyeblink response to light, one lobe (occipital) was ablated and he was then tested without the unconditioned stimulus. The animals displayed perfect retention. After receiving fifty presentations of

the unconditioned stimulus the second lobe was removed and he was again tested. For the second time, the animal showed retention. This procedure, employing a two stage operation and exposing the animal to the training situation between the two operations, limits the generalization concerning postoperative retention.

The animal showing no retention suffered removal of both lobes before being tested. A third monkey got 60 per cent correct responses when tested after removal of the first lobe and without further training was deprived of the second occipital lobe. The test after operation showed complete amnesia for the problem. The authors ascribe the loss of the habit in the latter two animals to the effect of shock to other centers.

Wing and Smith (21) used the instrumental avoidance conditioning technique in training dogs to respond to a light stimulus. The animals were strapped in a conditioning stand with a hind leg free to move several inches from the platform. The conditioned stimulus consisted of a light placed directly before the animal. The unconditioned stimulus was an electric shock applied to the leg of the dog by means of electrodes held in a cuff and fixed to the leg. The dogs were able to avoid the shock by lifting the leg at the onset of light or during the first two seconds of the

3.3 seconds that the light remained on. If the dogs failed to respond, shock was administered. Random responses during trial intervals were punished by a tap on the dog's leg.

The animals received 25 trials per day until a criterion of 18 correct responses out of 20 consecutive trials was attained. This was followed by extinction and reconditioning of the response. The animals then underwent bilateral removal of the striate area. Approximately two weeks after operation they were returned to the training stand and tested.

Retention was measured by reconditioning (method of saving) and extinction. One dog gave 100 per cent conditioned responses, that is, it achieved criterion without a single reinforcement. Other animals required from two to three days training (25 trials per day) to reattain criterion. The number of reinforcements varied from zero to seventeen.

In the extinction series which followed, one animal failed to extinguish after 25 days (553 trials) although preoperative extinction took place within 5 days (120 trials). Other animals required from two to three times the number of extinction trials after operation as originally required for extinction preoperatively. These slow extinction rates complicate the assessment of postoperative retention. Wing (19) used essentially the same training methods. The animals

were trained to a criterion of 90 per cent responses on two successive days. Each animal received a series of extinctions and reconditionings prior to operation. The experiment involved training two of the animals to the onset of light and three to an increase in intensity of the light stimulus. The two dogs trained to onset of light retained the response after operation. These animals had partial lesions of the cortex. One of the three animals trained to increase in intensity underwent complete ablation of the striate area. This animal did not retain the response when measured postoperatively as far as direction of light change was concerned. The dog responded as often to decrease in intensity as to increase in intensity. However, the animal was not tested prior to operation to the decrease in intensity and hence the absence of the correct response after operation cannot be ascribed conclusively to the removal of the striate cortex.

The second study conducted by Wing (20) involved nine dogs. Three of the animals were conditioned to the onset of light, three to increase in intensity, and three to decrease in intensity. Since no two animals received exactly the same training only the general procedure is reported here. The instrumental reward technique was used in the experiment. The training situation previously described was modified in such a way that leg flexion in

response to the conditioned stimulus rewarded the animal with food. The initial learning situtíon required the experimenter to forcibly lift the dog's leg via a rope and pully system when the conditioned stimulus was presented. This procedure was discontinued once the animal had learned. Those dogs trained to a decrease in intensity were brought into the conditioning situation with the stimulus panel lighted at an intensity denoted here as S1. The conditioned stimulus consisted of a decrease in light intensity to a value S2.

In the test situation, the dogs were brought to the conditioning stand with the light at the decreased intensity, S2, the onset of which formerly served as the conditioned stimulus. The light, S2, was then increased to intensity S1, for three seconds, and then reduced to S2. The correct response consisted of responding only to the decrease in intensity, that is, the change from S1 back to S2.

Three animals had specific training to the direction of light change. The training consisted of series I of ten trials in the normal conditioning procedure, followed by series II which reversed the conditioned stimulus for ten trials. The animals in this case, as previously reported in describing the test situation, entered the conditioning stand with the conditioned stimulus panel lighted to an

intensity equal to that formerly serving as the conditioned stimulus, S2, and when the light increased to intensity S1, the animal was not reinforced if he responded. The return to the original intensity at the end of the 3.3 seconds constituted a decrease in intensity and response at this time was reinforced. On the second training day, the order of presentation of the series was reversed. The animal now received series II followed by series I. The procedure was continued for several days and was followed by still another schedule. The animals under the second schedule received five to ten trials without reinforcement following the procedure of series I mentioned above. This was followed by ten reinforced trials using the procedure of series II. A third series was introduced and the three series were presented in reverse order on alternate days for some unspecified number of days.

One animal, receiving specific training to direction of light change, underwent total ablation of the visual area. This animal did not retain the response after operation. That is, there was no significant difference between the percentage of responses to the increase and decrease in light intensities. However, the large day to day variation in the number of conditioned responses prior to operation makes it generally difficult to evaluate the degree of retention postoperatively. From the study, Wing (20, p. 67) concludes,

"The striate area plays an essential role in the retention of the differential aspects of discriminatory responses based upon a particular kind of difference in brightness or intensity of light, but not in the retention of conditioned responses to such differences in general."

From a study by Marquis and Hilgard (8) one would not expect the loss of the response to be due to change in threshold of the animal. That the animal can detect the changes in intensity is demonstrated by his behavior, however, the appropriate behavior associated with each intensity appears wanting. A complicating factor, the effects of which are not easily isolated, is that the animal in the test situation is presented with a light stimulus the change to which formerly served as a conditioned stimulus but which now serves as the background stimulus.

Though Wing's investigation is concerned with discrimination, in the more restricted meaning of the word, the complexity of the experimental situation does not allow one to state whether the striate area of the cortex is essential to the retention of a conditioned differentiation of two lights. The work by Wing suggests that a differential response to two different light intensities would not survive removal of the visual area, and hence leads to the conclusion that the visual cortex plays an essential role in the

performance of a differential response to two light stimuli.

Unfortunately, the evidence on which Wing based his conclusions is not always clear. For example, one animal trained to the onset of light failed to extinguish after several hundred trials given preoperatively. After total removal of the striate area the animal again failed to extinguish when tested. The preoperative failure to extinguish leaves obscure the meaning of the postoperative results.

In another instance, an animal with partial lesions to the striate area gave a lower score on postoperative extinction test than animals with complete lesions. This would suggest that some animals with partial lesions suffer greater loss than animals with complete ablation. This is unaccounted for in Wing's conclusions.

An added difficulty is that each animal received different preoperative training in addition to different postoperative tests. These differences occur within each of the three groups of animals trained to different conditioned stimuli as well as between the groups.

This evaluation is not offered as a criticism of Wing but is presented as evidence for the need of further investigation in the area.

CHAPTER III

STUDY I

EXPERIMENTAL METHODS

The present study was undertaken to confirm and clarify the findings of previous studies regarding the effects of partial lesions of the striate cortex on previously learned conditioned avoidance responses. To demonstrate, moreover, that the operation acted specifically upon the visual conditioned response, the animals were trained to an auditory stimulus as well as to the visual stimulus. The same response was required in both cases. Postoperative loss of response to the visual stimulus without accompanying loss to the auditory stimulus would indicate that only visually determined behavior had been affected. This information together with preoperative retention scores for the conditioned responses to the two stimuli provided maximum control.

<u>Experimental</u> <u>Animals</u>. The cat, though often used in neurological research is seldom employed in psychological investigations. This animals was chosen since it appeared to avoid many of the difficulties and extensive facilities required for working with dogs, and at the same time was large enough to simplify the operative difficulties encountered

with rats because of that animal's small brain size. In addition, it provided an opportunity to explore the possibilities of the cat as a laboratory animal for further use in psychophysiological research.

The animals used in this study were three, mature, male cats and one, young adult male. All were experimentally sophisticated and had been previously conditioned to a visual conditioned stimulus and were adjusted to the general experimental conditions.

The animals were fed canned cat or dog food twice daily. Every other day they were given evaporated milk diluted with water. Drinking water was present in the cages at all times. The cages in which the animals were housed measured approximately 36 inches by 30 inches by 24 inches.

An exercise period of about one hour a day was allowed. The animal was permitted to move about the experimenter's room.

Apparatus. The training apparatus consisted of a rectangular box (31 inches by 12 inches by 6 inches) supported on two glass rollers and free to move along its longitudinal axis about an inch in either direction. Springs returned the box to its neutral position. The floor of the box consisted of a wire grid which could be electrically charged.

Two switches (S.1 and S.2) were attached to one end of the box. A movement of the box in either direction of more than .125 inches closed both switches. The stimulus light and a buzzer were located one foot above and to one end of the training box. The box was situated in a completely dark training room except when the light stimulus was on.

Any motion of the animal which moved the box sufficiently to close the switch constituted the response used in this study.

All responses made by the animal, whether during or between trials, were recorded by a response counter which provided a measure of the general activity level of the animal. A microphone placed near the training box with an amplifier and loud speaker situated in the experimenter's room provided an additional check on the animal's activity.

The arrangement of the apparatus is shown schematically in Figure 1.

Automatic trial and session timing equipment was located in the experimenter's room. The trial timer controlled the application of the conditioned stimulus and the electric shock (unconditioned stimulus). The trial timer was normally started by the session timer but could also be started manually by briefly pressing a key. The CS-US interval, as well as the length of the trial, was automatically controlled

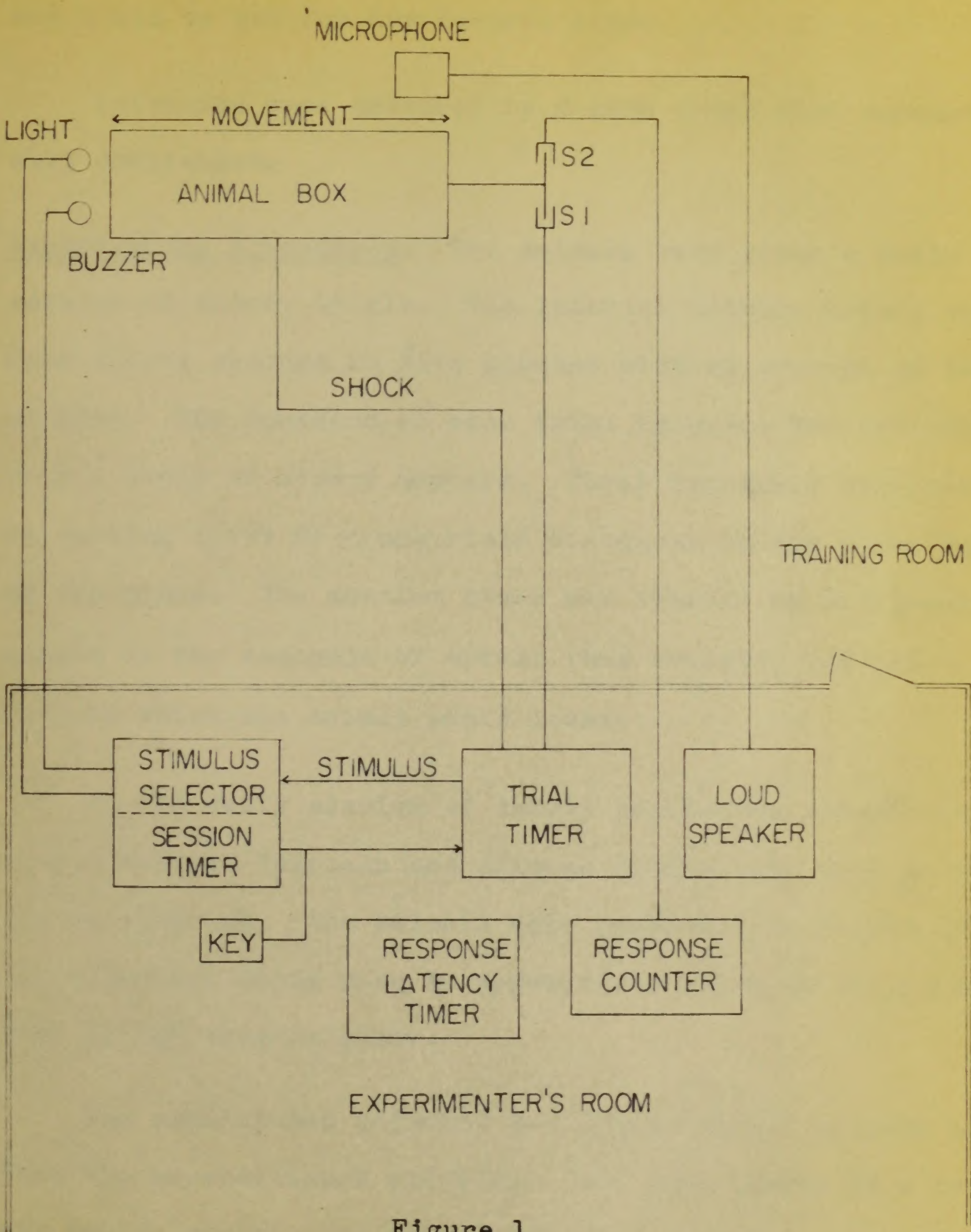

Figure 1

Schematic diagram of the training apparatus. The apparatus in the experimenter's room was housed in a soundproof box.

and could be set for any desired time.

Latencies were measured by a stop clock also automatically controlled.

Experimental Procedures. The animals were given a daily session of thirty trials. The interval between trials varied from thirty seconds to five minutes with an average of two minutes. The duration of each trial interval was selected from a table of random numbers. These intervals were set by cutting slits at appropriate distances in the paper tape of the timer. The session timer was started at different points in the sequence of trials thus avoiding any set pattern which the animal could learn.

In the daily session of thirty trials the animal received between fourteen and sixteen trials with each conditioned stimulus. The stimuli were presented in random order, the selection being made by appropriate slits in the paper tape of the session timer.

The conditioned stimulus was presented 2.8 seconds before the unconditioned stimulus. The full length of a trial was twelve seconds and the conditioned stimulus and unconditioned stimulus were applied for the duration unless the animal responded earlier. The shock supply was set to deliver a constant current of 2 milliamperes. If the animal

responded in less than 2.8 seconds, the conditioned stimulus and the shock supply were turned off automatically. The unconditioned stimulus was thus avoided and the response constituted a conditioned response. If the animal's response was delayed more than 2.8 seconds but occured before the end of the trial, both the conditioned stimulus and the unconditioned stimulus were automatically turned off. Such a response constituted an unconditioned response.

The latency of the response was recorded from a stop clock which measured the latency of both the conditioned response and the unconditioned response.

It was merely necessary for the experimenter to place the cat in the box, start the session timer and record the response latency of each trial. The apparatus thus provided completely automatic training of the animal. At the end of the session the animal was removed from the box and returned to his home cage.

The animals received thirty trials a day for ten to fifteen days. A minimum of three hundred trials with a variation of less than four conditioned responses in the daily score in either task over at least six days was used as the learning criterion. One animal received two days additional training but the animal died before being tested

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The latency of the response was recorded from a stop clock which measured the latency of both the conditioned response and the unconditioned response.

It was merely necessary for the experimenter to place the rat in the box, start the session timer and record the response latency of each trial. The apparatus thus provided completely automatic training of the animal. At the end of the session the animal was removed from the box and returned to his home cage.

The animals received thirty trials a day for ten to fifteen days. A minimum of three hundred trials with a variation of less than four conditioned responses in the daily score in either task over at least six days was used as the learning criterion. One animal received two days additional training but the animal died before being tested

and hence had no effect on the final evaluation.

After reaching criterion the animals were allowed a rest period of 53 to 61 days. During this period the cats were maintained on the same feeding and exercise schedule. At the end of the rest interval the animals were given fifteen trials in the apparatus with the shock supply disconnected. Additional training trials were given on succeeding days to restore the animals to their original response level.

The day following the last of these additional training sessions the animals underwent surgery. Between ten and fourteen days later all animals were given fifteen test trials in the apparatus with the shock supply disconnected. Varying amounts of extinction and reconditioning were given to two cats. At the conclusion of the various test sequences, the animals were sacrificed and the brains examined.

Preoperative Retention Control. The preoperative retention test consisted of fifteen extinction trials divided between two conditioned stimuli. The number of trials to each stimulus varied because of the random manner in which the session timer determined the particular stimulus to be presented. The session timer was constructed so as to produce fifteen trials to each of the two stimuli in a random manner for a session of thirty trials.

The response latencies of the first half of the last training session prior to the waiting period were taken as representative of the response level attained by the animals. These latencies were compared with the latencies of the first half of the test trials to the visual and auditory stimuli, given following the waiting period. The first half of the sessions was employed rather than the entire session to avoid including the effect of extinction on the determination of retention. Using a one-tailed test, the 5 per cent point was taken as significant. The Mann-Whitney U Test, as described by Moses (10) was used to evaluate the results.

Postoperative Test of Retention. The postoperative test of retention followed the same procedure adopted for estimating retention following the rest period. In addition, two of the animals received reconditioning trials, thus making available an estimate of savings following operation.

Surgery. The operations were carried out under general Nembutal anesthesia. The operative site was cleaned and shaved. A longitudinal incision was made along the midline over the sagittal suture and extending caudad to just over the occipital bone. The skull was opened with bone rongeurs to expose the posterior half of the cerebral hemispheres. The dura was reflected and the cortex removed by the aspiration method. Care was taken to avoid the large blood vessels

lying over the area. The lesions were confined to the projection of the lateral geniculate body upon the cortex (18). The wound was closed in three anatomical layers.

The wound was dusted with sulfa-nilamide. Procaine penicillin (150,000 units) was given for two days prior to operation and for seven days after operation.

One cat died within twelve hours of the operation. This animal had excessive hemorrhage from the bone and also received longer maintaining doses of Nembutal than the other animals. The remaining three animals recovered without incident.

Within two days of the last test trial each animal was killed by an overdose of Nembutal and the brain removed. The brains were fixed and stored in 70 per cent alcohol.

CHAPTER IV

RESULTS

STUDY I

Initial Learning. The animals had learned the visual conditioned response in a prior experiment and there was little change in their performance of this task during the training sessions. The acquisition of the auditory conditioned response was rapid. Criterion was reached within fifteen sessions (450 trials) in all animals. The acquisition curve of a typical animal is shown in Figure 2.

Preoperative Retention. Table I shows that the percentage of conditioned responses for the preoperative extinction test varied from 85 per cent to 100 per cent for the visual stimulus and was 100 per cent in all animals for the auditory stimulus.

The response latencies for the test session were not significantly greater ($p > .05$) than the response latencies of the last preforgetting session.

In view of these findings it was expected that the same results would hold postoperatively unless the operation was a significant factor. A significant increase in response latency or a precipitous drop in the percentage of conditioned responses following operation would be ascribed to

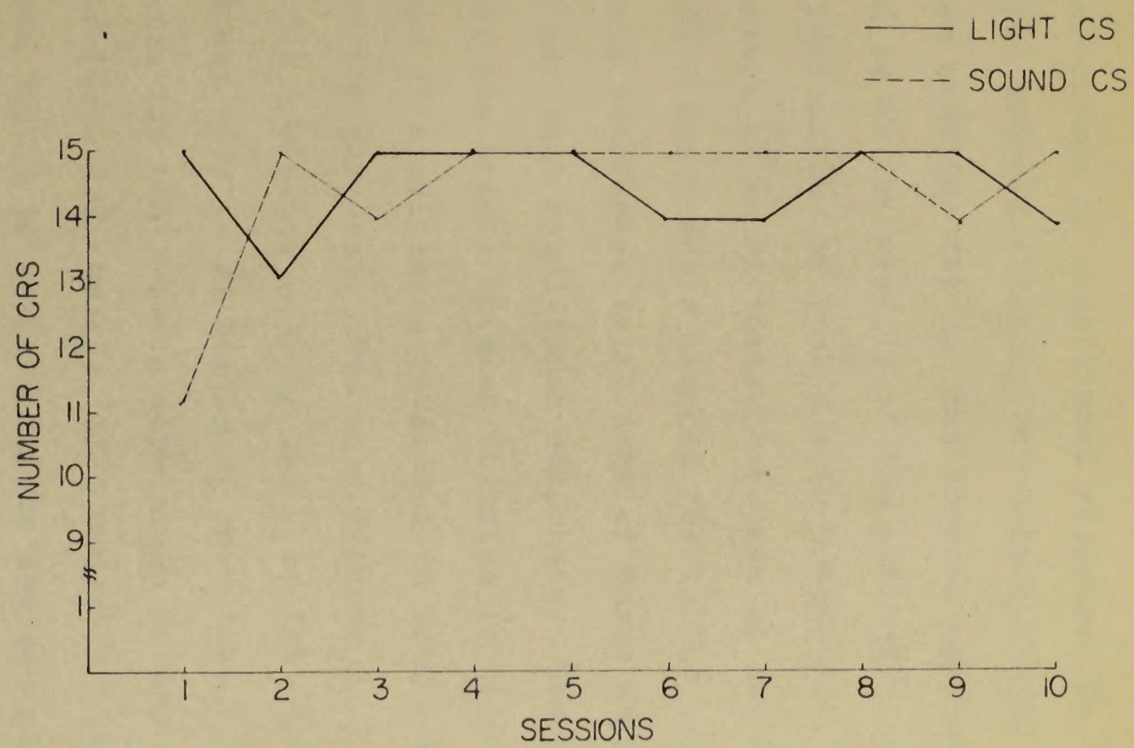

Figure 2

Learning curves of a typical animal (Cat 2.). Each session consisted of thirty trials, half to each stimulus.

the effect of operation.

Effects of Operation. The effect of the operation on the retention of the conditioned responses is shown in Table I. The percentage of conditioned responses to the auditory stimulus dropped slightly for Cats 3 and 4, but remained at 100 per cent for Cat 2. The lowered percentages are considered to be the results of the extinction process rather than indications of loss due to operation. The lowered percentage of conditioned responses to the visual stimulus by Cats 2 and 3 are accounted for in the same manner. With a single reinforced trial both of these animals reattained a 100 per cent conditioned responses. When only the first half of the trials to each stimulus is considered, the percentage of conditioned responses to both stimuli is approximately 100 per cent. See also Figures 2, 3, and 4.

The low score made by Cat 4 to the visual stimulus is based not only on latencies of more than 2.8 seconds, which accounts for the lowered percentage of the other two cats, but includes four trials (of a possible eight) in which the animals failed to respond in the twelve seconds in which the light stimulus remained on. A vestage of the habit is seen in the few conditioned responses the animals did make. Unfortunately, the animal was not given retraining trials.

The effects of the operation were also examined in terms of the latency of response to the two stimuli. These

results are shown in Figures 3, 4 and 5. The latency of each response in the last preoperative session is plotted and is followed by the latency of response in the postoperative test session.

The Mann-Whitney U Test was applied to determine whether the latencies of the first half of the postoperative retention responses was greater than the latency of the responses in the first half of the last preoperative session. The results indicate that the response latencies to the visual and auditory stimuli for Cats 2 and 3 and for the auditory response in Cat 4 were not significantly greater ($p > .10$).

In the postoperative test to the visual stimulus Cat 4 failed to respond on four of the trials (see Figure 5) and the latency of the four responses which the cat did make were all higher than the median of the combined preoperative and postoperative latencies.

The results of the U test comparing preoperative and postoperative response latencies appear in Table II.

The tendency for the visual and auditory conditioned responses to extinguish is apparent in the performance of Cat 3 (see Figure 4). At the conclusion of the fifteenth trial, which constituted the postoperative test session, the shock supply was reconnected and the animal was given five additional trials. As may be seen in Figure 4, the

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TABLE I

PERCENTAGE CONDITIONED RESPONSES TO THE VISUAL AND AUDITORY STIMULUS IN THE PREOPERATIVE EXTINCTION TEST AND IN THE LAST PREOPERATIVE AND FIRST POSTOPERATIVE SESSION

Cat	Percentage Conditioned Responses Preoperative Extinction Test		Percentage Conditioned Responses Last Preoperative Session		Percentage Conditioned Responses First Postoperative Session	
	Visual Stimulus	Auditory Stimulus	Visual Stimulus	Auditory Stimulus	Visual Stimulus	Auditory Stimulus
2	100	100	100	100	66.6	100
3	87.5	100	87.5	100	62.5	75
4	100	100	100	100	38.7	85.7

TABLE II

THE P VALUE OF RESPONSE LATENCIES IN THE FIRST POSTOPERATIVE TEST SESSION AS DETERMINED BY THE MANN-WHITNEY U TEST

Cat	P of Visual Response Latencies	P of Auditory Response Latencies
2	Greater than .10	Greater than .10
3	Greater than .10	Greater than .10
4	.001	Greater than .10

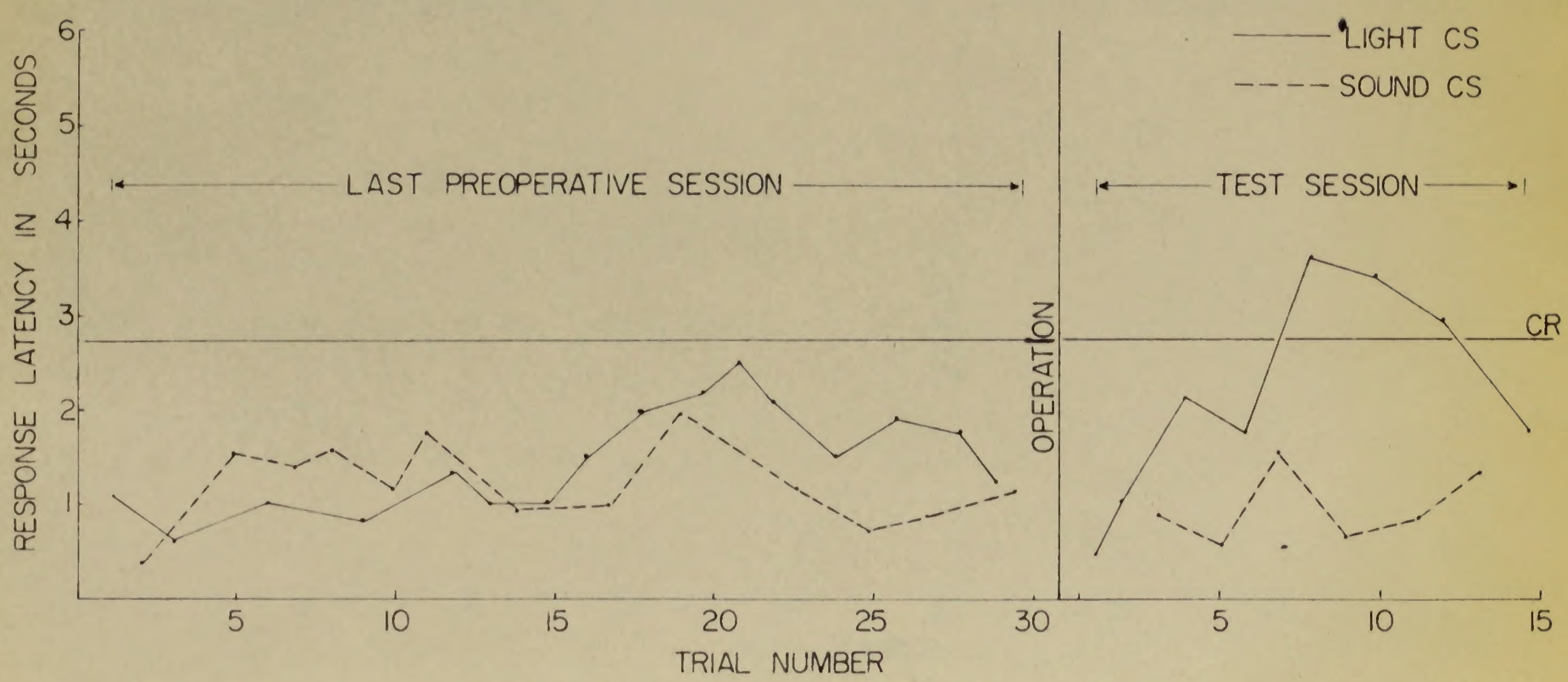

Figure 3

Cat 2. Response latencies during the last preoperative training session and the first postoperative test session. The shock supply was disconnected during the test session.

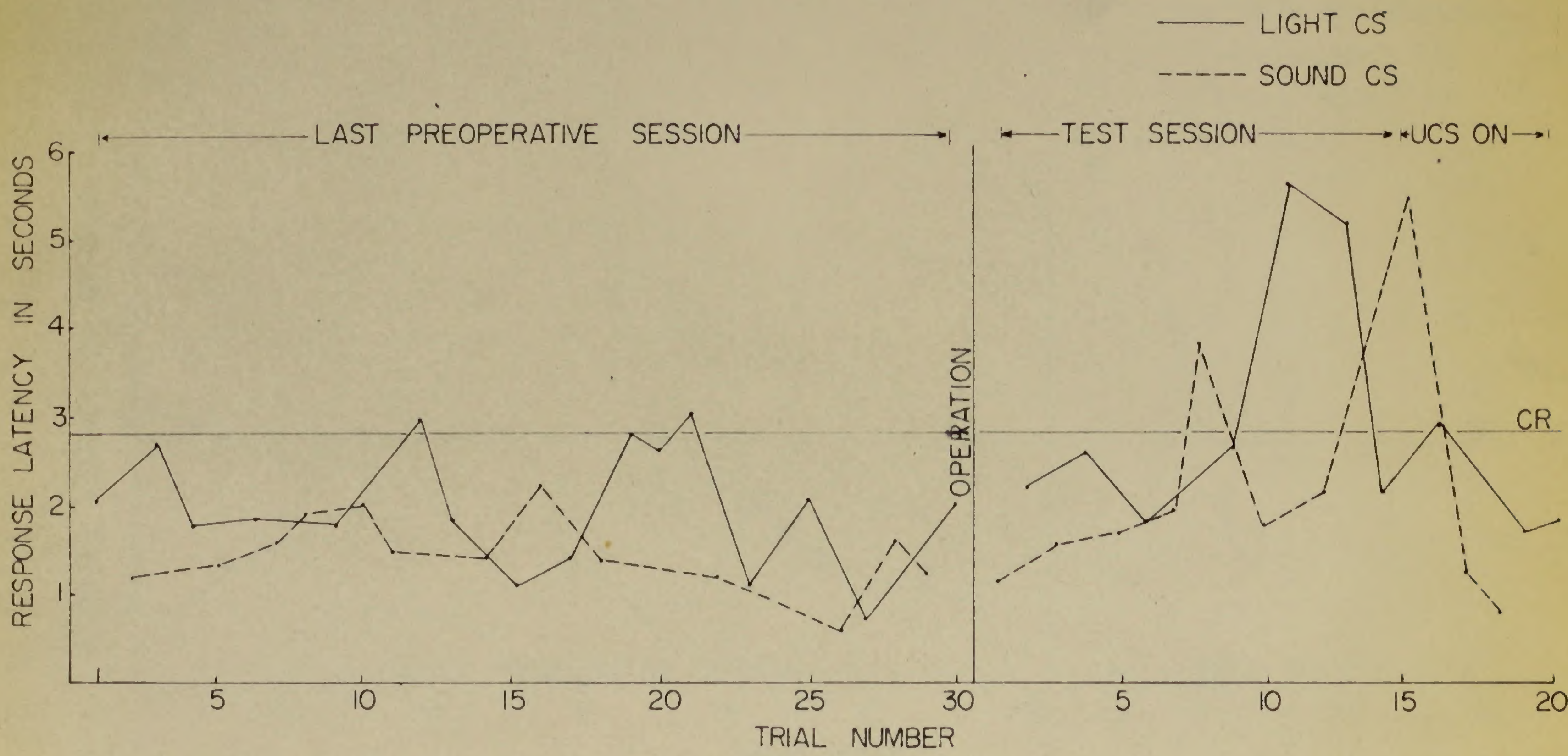

Figure 4

Cat 3. Response latencies during the last preoperative training session and the postoperative test session. The shock supply was disconnected for the first fifteen trials of the test session and reconnected on the sixteenth trial (UCS on).

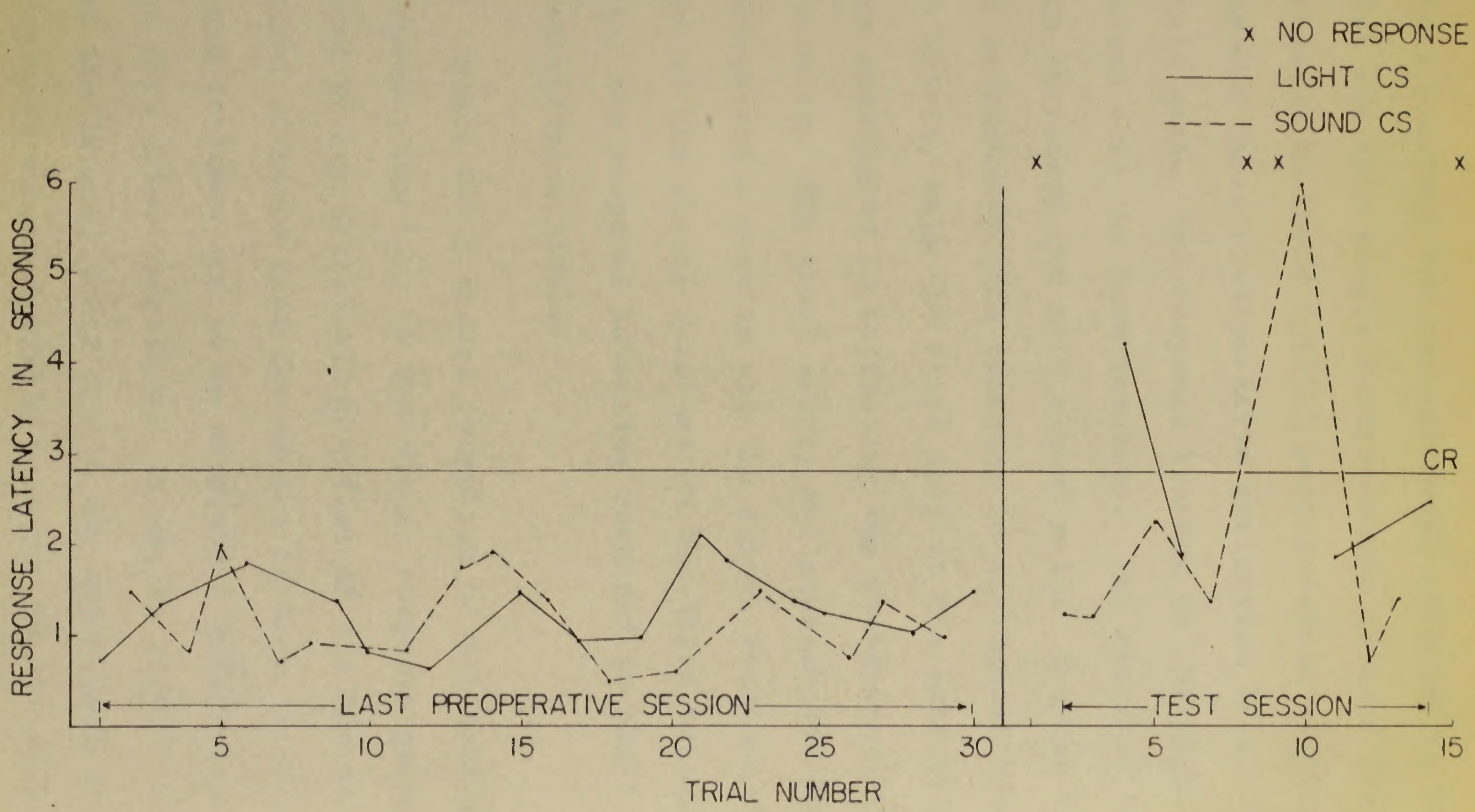

Figure 5

Cat 4. Response latencies during the last preoperative training session and the postoperative test session. The shock supply was disconnected during the test session.

animal received the unconditioned stimulus on the sixteenth trial and this single reinforcement lowered the response latencies to their initial postoperative values. Cat 2 received three postoperative extinction sessions of fifteen trials each. The response latency to the light steadily increased over the test sessions. The response to the buzzer also increased but at a slower rate. Because the animals did demonstrate this tendency to extinguish after the first few trials, only the first half of the extinction trials were considered in estimating the postoperative response latencies. The shock supply was reconnected for a fourth postoperative session and the animal received a reinforcement of the visual response on the third trial. Following this, the response latencies returned to their initial postoperative level.

Since Cat 4 showed retention of the conditioned auditory response, the loss of the visual response cannot be attributed to any debilitating effect of the operation. This animal differed from the others in that it appeared to have large scotomas and to be completely blind during the first two days after operation. It may be significant that Cat 4 had the largest total day to day variations in conditioned responses during training period. He was also the only animal that failed to achieve criterion by the end of the minimum number of required trials.

The results, based upon the findings with Cats 2 and 3, indicate that an avoidance conditioned response may be quite unaffected by subtotal lesions to the visual cortex.

The operative lesions drawn with the aid of a camera lucida are shown in Figure 6. The lesions are confined to the striate cortex as indicated by Waller (18). The superior and inferior colliculi were undamaged in all animals.

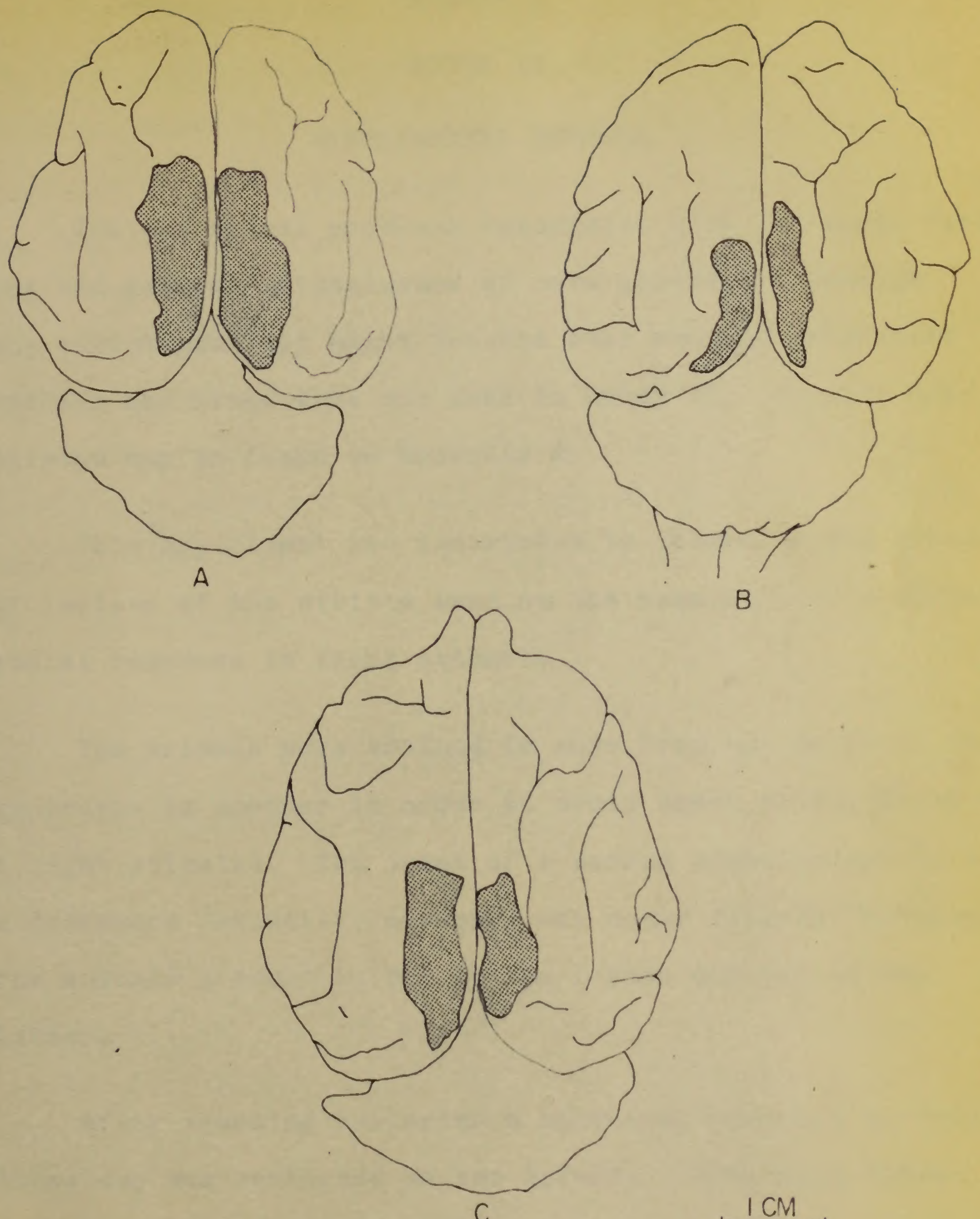

Figure 6

Camera lucida drawings of cats' brains made at necropsy. Pictured in A, B and C are the brains of Cats 4, 3 and 2, respectively. Hatched areas indicate extent of cortical lesion.

CHAPTER V

STUDY II

EXPERIMENTAL METHODS

The additional problems associated with the care, feeding and general maintainance of cats proved to outweigh any advantages they might possess over rats as laboratory animals and hence were not used in Study II. Further discussion may be found in Appendix A.

This experiment was undertaken to determine the effects of lesions of the striate area on the retention of a differential response to light stimuli.

The animals were trained to move from one point in the apparatus to another in order to avoid shock at the onset of a light stimulus. The onset of a second light stimulus, of a different intensity, however, was never followed by shock. The animals learned to run to the former and not to the latter.

After reaching criterion a bilateral subtotal occipital lobectomy was performed on the animals. They were subsequently tested for retention.

A number of preliminary studies were required to find an adequate training apparatus; to determine suitable training procedure and develop efficient operative techniques.

These exploratory studies investigated such variables as shock intensity, inter-trial interval, number of daily trials, sequence of stimulus presentations, anesthetic dose and operative technique. For a review of these studies see Preliminary Studies in Appendix A.

Subjects. The subjects consisted of twenty-four experimentally naive, young male albino rats weighing between 160 and 180 grams at the beginning of the experiment. The rats were housed in individual cages 7 inches by 7 inches by 12 inches. They were kept on a self-feeding schedule with water available at all times.

On coming into the laboratory the animals were weighed, divided randomly into five groups and then marked by a system of differential slits on the ears.

Apparatus. The training apparatus used in the experiment was a modified design of a circular grid used by Mowrer (15, p. 66) and adapted by him from an apparatus originally described by Culler, Finch and Girden with later changes added by Hunter.

The apparatus consisted of a circular grid 5 inches wide and enclosed by transparent, 10 gauge acetate walls 22 inches high. The frame of the apparatus consisted of two wheels, 2 inches wide cut from 3/4 inch plywood. The outer

diameter of the smaller wheel was 18 inches and the inner diameter of the larger wheel was 28 inches. Thus the circumference at the outer wall of the grid runway measured approximately 88 inches. The grid was divided electrically into six sectors, any of which could be energized by a mercury selector switch.

The outer lip, 2 inches wide, was painted white and the six sectors were marked by black tape 1/2 inch wide placed on the upper surface of the rim. The "hub" of the wheel, or inner circle, was completely covered by a white cardboard which hid the wire connections and gave the center a uniform appearance. A picture of the apparatus appears in Figure 7.

The positive light stimulus (Sp) and the negative light stimulus (Sn) were suspended 23 inches above the center point of the apparatus. The two light bulbs were enclosed in a metal tube 7.5 inches in diameter. The lower end of the tube was covered by a ground glass plate. The light bulbs were placed 12 inches from the plate and were provided with an aluminum foil reflector for diffusing the light. Uniformity was further aided by the white inner surface of the tube. The illuminance values of the two light stimuli were approximately .0075 foot-candles and 14.5 foot-candles.

There were several features of the apparatus which made it particularly well suited to the problem investigated.

Figure 7

The training apparatus.

The response the animal was required to make did not necessitate any specific directional body orientation. The animal could run in either direction in order to execute the correct response. There were no obstacles which animal could encounter in running such as barriers to jump or doors through which he was required to pass. This study, investigating retention of responses to light intensity and not retention of responses based on pattern vision, avoided using a response which required the animal to locate or manipulate a device such as a bar.

Since no one visual pattern constituted an adequate stimulus for executing the correct response, the changes in light intensity remained the only appropriate cue which could serve as a basis on which to solve the differentiation problem.

The apparatus did not require the handling of the animal between trials and once placed in the apparatus the animal was free to move about.

The training room contained the apparatus which was placed on two supporting arms 9.5 inches above the floor. The experimenter's table and chair were located across the room from the circular grid.

An instrument panel on the experimenter's table contained: a set of mercury selector switches for energizing the

various sectors of the grid, a stop clock for recording latencies, a meter indicating current flow through the shocking circuit, a key for recording responses and a switch for terminating the trial. The last mentioned switch was connected so as to turn off the conditioned stimulus, open the shock circuit and stop the clock.

There were two dim lights on in the training room throughout the experimental sessions. One light was located approximately ten feet above the apparatus and arranged so as to diffuse the light symmetrically at the apparatus end of the room. The second light on the instrument panel was just bright enough to allow the experimenter to read the clock and record the time.

The power supply, a trial timer, counter and relays were located in a sound proof box in the experimenter's room.

The arrangement of the apparatus is shown schematically in Figure 8.

The shock circuit consisted of a thousand volt D.C. power supply with fixed resistance in series so as to deliver approximately .4 milliamperes of current through the animal when he stood on alternate grids of the apparatus.

The interval between trials was determined by slits cut

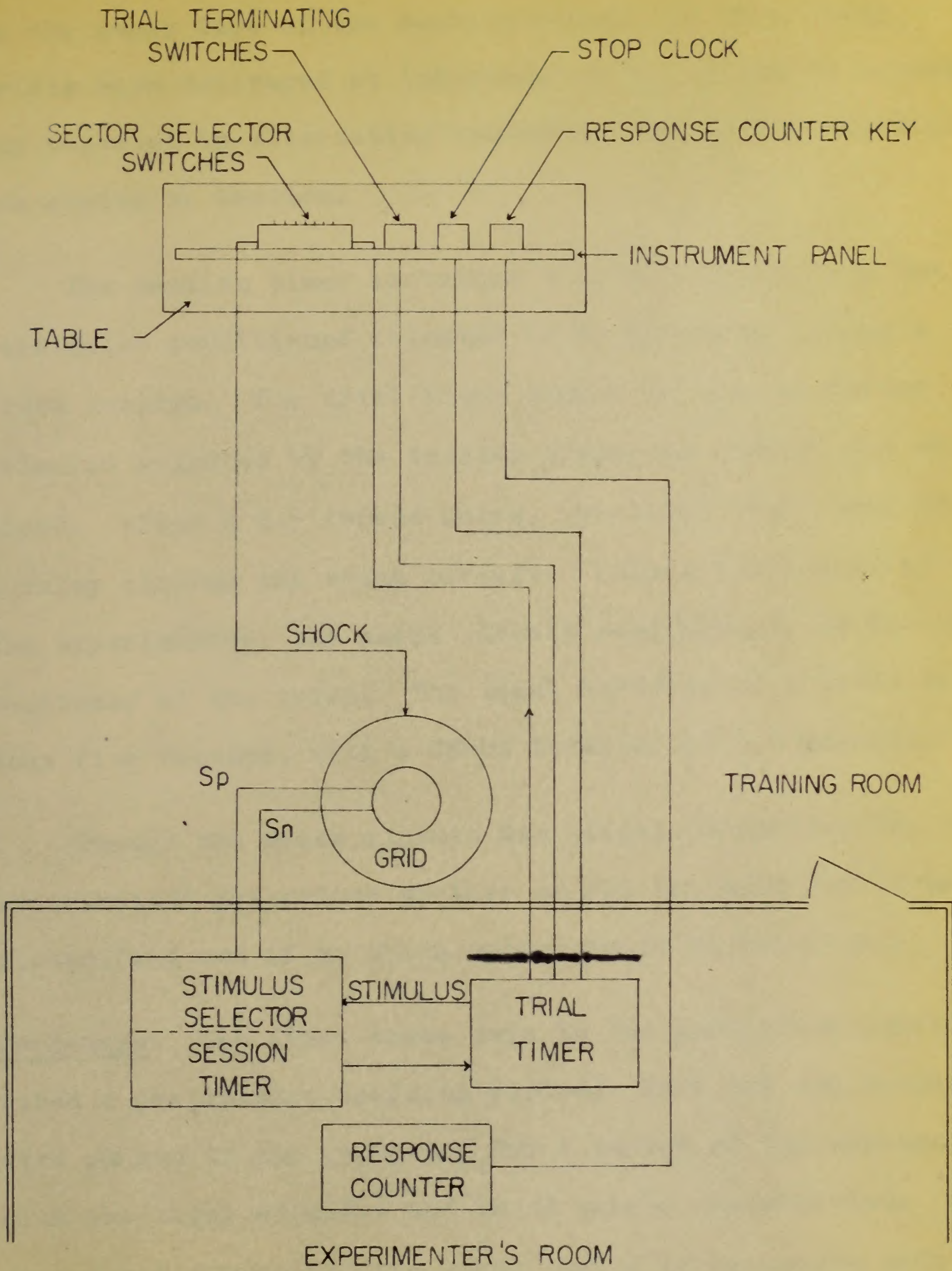

Figure 8

Schematic diagram of training apparatus. The instruments in the experimenter's room were housed in a soundproof box.

in the paper tape of the session timer. In this study, trials were delivered at intervals of 30, 45 and 60 seconds and repeated in alternating sequence. Ten trials constituted one series or session.

The session timer contained a switch controlling the particular conditioned stimulus to be presented during a given session. The trial timer turned on the particular stimulus selected by the session timer and started the stop clock. After a 2.5 second delay, the trial timer activated a relay closing the shock circuit. Unless terminated by the experimenter, the shock circuit remained closed for the remainder of the trial. The total duration of a trial was thus five seconds, with a CS-US interval of 2.5 seconds.

Though the shock circuit was closed automatically, the experimenter determined whether or not the grid was to be electrified and if so which sector would be energized.

<u>Procedure</u>. The first three days in the laboratory constituted a preliminary training period. Each day the subjects were placed in the apparatus for a period of ten minutes with the light stimulus and shock supply disconnected. The experimenter recorded the total number of responses made by the rat. A response is defined as the rat crossing a line separating adjacent sectors of the apparatus.

Training to the positive stimulus (Sp) was carried out in the following manner. The animal was placed in the apparatus through the top which was not covered. Though the rat was placed on the same sector at the beginning of each session, the direction which he faced was varied from session to session. The animal was allowed to remain in the apparatus for one minute before each session started. The period was introduced to allow for initial exploratory activity. Responses during this minute were not counted in the session total.

The session timer was started and the appropriate stimulus selected. The shock circuit was closed automatically 2.5 seconds after the onset of the Sp. The experimenter simply selected the sector to be electrified, that is, the sector on which the animal stood at the onset of the Sp, by closing the appropriate switch. In the event the subject was spanning two adjacent sectors, both sectors were electrified.

If the animal did not respond within 2.5 seconds after the onset of the Sp, he received the shock and could escape by running to another sector. At the instant the hind legs of the animal passed off the energized sector of the grid, the meter needle fell to zero and the experimenter threw the switch that turned off the Sp. Though the subject escaped

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the shock by going to a different sector which was not electrified, the operation which turned off the Sp also opened and reset the shock circuit for the next trial. This avoided the possibility of having the animal return to the energized sector and receiving a shock at any but specified times. If not opened in this manner, the circuit would remain closed for five seconds, the duration of a trial. This same switch was so connected that it stopped the clock which was started automatically at the onset of the Sp. The experimenter recorded the latency of the responses, here defined as the time lapse between the onset of the Sp and the animal's response.

If the animal moved from one sector to another before 2.5 seconds and avoided the shock, the response was considered a conditioned avoidance response. The Sp was terminated at the moment of the response as before and the time recorded.

Preliminary investigation revealed that the proximity in time of the trial to the Sp and the trial to the Sn greatly affected the extent of generalization from one stimulus to the other. When the inter-trial interval varied from thirty seconds to one minute with the Sn and the Sp presented randomly through the series, the animals failed to meet criterion after receiving over three hundred trials.

See Appendix A. For this reason, the Sn and the Sp were presented in blocks of ten trials each.

On each experimental day the animals were given two sessions both consisting of ten trials. The first series consisted of ten trials to the Sp and the second series, given five hours later, was made up of ten trials to the Sn. On each succeeding day of the training period, the order of presentation of the stimuli was reversed such that on the odd numbered days the negative series followed the positive while on the even numbered days the positive series followed the negative. The order of the series ran Sp, Sn; Sn, Sp; Sp, Sn....

Training to the negative stimulus (Sn), the differential stimulus, followed the same general procedure employed in training to the Sp. The animals were placed in the apparatus for one minute before the session started and the same inter-trial intervals were used.

The Sn, which came on automatically, was allowed to remain on for five seconds regardless of the animal's response. After five seconds, the Sn was automatically turned off. In no case was the animal shocked during these sessions. The moment the animal crossed from one sector to another, after the onset of the Sn, the clock was stopped and the time recorded. Any response which carried the animal from one sector to

another within 2.5 seconds of the onset of the Sn was considered an error, that is, the animal made a generalized conditioned response to the negative stimulus.

Criterion of Learning. Training as described was carried on until a differentiation of the two light intensities was established. Animals making less than 50 per cent conditioned responses atthe end of seven daystraining (140 trials) or who failed to reach criterion after twenty-five days (500 trials) were discarded. The animal was considered to have differentiated the stimuli when he ran from the sector within 2.5 seconds and failed to run from the sector within 2.5 seconds when the Sn was presented. The occurence of more than one response to the Sn in a session was considered as evidence of generalization. The figure is based upon a preliminary investigation which sought to obtain an estimate of the basic response rate of the rat.

A rat was placed in the apparatus, the light and shock circuits were disconnected and the session timer started. At intervals determined by the session timer, the clock was started. The experimenter stopped the clock the moment the rat moved from one sector to another and recorded any response occuring within the 2.5 second interval. An average of less than one such response was recorded per session. A session consisted of ten trials. The animals used were

given one session per day for three days.

The criterion of differentiation or of learning consisted of eight successive sessions with at least 80 per cent conditioned shock avoidance respones to the Sp and no more than 20 per cent such responses to the Sn. A response within 2.5 seconds of the onset of the Sn constituted an error, and failure to respond within the same time period to the Sp was also considered an error.

Response Latency. The latency of each conditioned response and of each generalized conditioned response was recorded throughout the experiment. The latencies were recorded in hundreds of a second. In the event an animal failed to respond within five seconds, the duration of a trial, he was given an arbitrary score of five.

A response latency of 2.49 seconds or less to the Sp constituted a conditioned response and a latency of 2.49 seconds or less to the Sn constituted a generalized conditioned response.

Total Locomotor Responses. The total number of responses made by each animal during each session was recorded, with the exception of responses occuring during the first minute of each session. Conditioned responses, as well as generalized conditioned responses, were included in the session total.

The count was kept as an indicator of total activity and as evidence that the number of conditioned responses was not directly related to the total number of responses occuring in a session.

Retention Tests. All animals except the blind controls of Group I were given two tests of retention.

Test I. The animals were placed in the apparatus in the usual manner and were given ten trials to the Sp but with the shock circuit disconnected. Five hours later they were returned to the apparatus and given ten trials to the Sn and, as was true in the training situation, the grid was not energized.

To avoid ambiguity, the procedure is stated in terms of the operations involved rather than being simply called "extinction trials". The trials to the Sn never involved shock to the animal in the initial training nor was shock administered in the test trial. To speak of the latter as extinction trials would only serve to confuse. The entire training process involved, in the broadest sense of the term, the "extinction" of the generalized response to the Sn. Presenting the Sp and withholding the shock stimulus may accurately be called an extinction trial. The extinction of this response could be expected to affect the amount of generalization to the Sn. The direction of change over a period of time would be to lower the amount of generalization. Thus,

in this restricted sense, "extinction" of the response to the Sp would also indirectly tend to "extinguish" the generalized response to the Sn. Since the problem was one of differentiating two light stimuli by requiring the animal to respond to one of the stimuli and not to the other, it was necessary that the animal respond to the Sp. The response to the Sp was required in order to interpret the absence of generalized conditioned responses to the Sn in Test I.

The Wilcoxon T Test was performed to determine whether the response latencies in Test I to the Sp were significantly greater than the response latencies of the last postoperative session.

Test I was also given to three animals following a five day "forgetting" period. The Wilcoxon T was applied in a similar manner to determine the effect of the "forgetting" period on the latency of response of the two stimuli.

Test II. On the second day retraining was begun. The first session consisted of ten trials to the Sn, followed five hours later by ten trials to the Sp, with the shock circuit connected as described in the initial training procedure. Training was continued until the animals reattained the learning criterion.

The amount of retention or savings was expressed in

percentage terms. The percentage was calculated by dividing the difference between the number of initial and postoperative trials to criterion by the number of trials initially required (12).

Test III. Four animals were given a series of trials comparable to those described in Test I, except that the daily sessions were presented for several days in an alternating sequence as employed in the standard training procedure. Animals 10, 17 and 18 started Test III the day following their last postoperative training. Rat 11 began the test two days after the last postoperative training trials.

The test was carried out in order to determine whether the conditioned response to the Sp would extinguish and to observe the effect of these tests on responses to the Sn.

EXPERIMENTAL GROUPS

Group I. Blind Control. This group consisted of two animals. They were blinded by eneculation of the eyes (see Surgery). Following a two day recovery period, they were given preliminary training. On completion of the preliminary training, regular training was started and was continued until they had received approximately twice the mean number of trials required by the other animals to reach criterion. The animals were then sacrificed by administration of an overdose of ether. The group was used to demonstrate that

the problem could not be solved without the use of visual cues.

Group II. Operative Control. The operative control consisted of a single animal. Within twenty-four hours after having reached criterion the animal underwent a control operation in which non-striate cortex was removed. For details and methods see Surgery.

Five days after operation the animal was tested. This control was employed to insure that the results found in the experimental group were not due to the removal of any but a restricted area of the cortex. The rat also served as the conventional control for trauma or any other debilitating factors associated with the operation such as the anesthetic.

Group III. Unoperated Retention Control. The retention control group consisted of three animals. After reaching criterion, they were allowed a five day period in which no training was given. At the end of this time, they were returned to the apparatus and tested.

When the test was complete, which involved reattaining criterion, two of the animals underwent bilateral removal of the striate area. Following a five day recovery period, they were again tested.

The third animal, held as an "extra" continued his

normal cage life for fourteen days after completing the retention test. This animal was retested according to the standard procedure, when all animals used had recovered from operation. Upon completion of the test, the striate area of the cortex was removed bilaterally. Five days later, he was tested for postoperative retention.

The group was used to give an indication of the amount of forgetting that could be attributed to the lapse of time under normal living conditions. In addition, the animals served as their own retention controls since they also underwent surgery.

<u>Group IV</u>. <u>Experimental</u> <u>Sp</u> <u>Bright</u>. This experimental group consisted of five animals. The animals were trained with the brighter of the two stimuli, as the Sp. After reaching criterion, the animals underwent operation. Following a five day recovery period, the rats were tested for retention.

<u>Group V</u>. <u>Experimental</u> <u>Sp</u> <u>Dim</u>. These animals, three in number, received the same treatment given Group IV except that the dimmer of the two lights served as the Sp.

<u>Surgery</u>. The rats were given an interperitoneal injection of Nembusen (Abbot) anesthetic (50 mg. per kg. body weight). The hair over the head was cut with animal hair clippers and the area cleaned.

An incision approximately 2.5 cm. long was made along the midline of the head extending approximately from a point over the coronal suture to somewhat caudad of the brain case. The muscle was cleared away and the skull opened by means of a small power drill. The greater part of the parietal bone and parts of the temporal and interparietal bone were cut away with a pair of plier type clippers. A small ridge of bone over the midline was allowed to remain intact. The ridge served as a protection for the longitudinal venous sinus lying directly below it.

After reflecting the dura an attempt was made to remove that part of the cortex corresponding to Waller's (17) area representing the cortical projection of the lateral geniculate body. This was accomplished by the aspiration method. All operations were carried out bilaterally.

Bleeding, when it occured, was stopped by applying small pads of Gelfoam soaked in normal saline. When serious bone bleeding occured, it was stopped with bone wax.

The incision was closed by means of wound clips. After giving the animal an intramuscular injection of (100,000 units) Duricillin (Lilly) he was returned to his home cage. The entire operation took approximately one hour. One animal died of hemorrhage two days after operation.

Eneculation of the eyes carried out on blind controls was performed under Nembusen anesthetic as described above. The eye muscles were cut and the optic nerve clipped; the eye was then removed intact and sulfa-nilamide was dusted over the wound. Little or no bleeding occured and the operation was completed in less than twanty minutes.

The control operation followed the procedure outlined for the experimental groups. The operation differed only in the portion of the cortex removed. In this instant, portions of the cortex receiving projection fibers from the lateral anterior nucleus were removed.

The animals were allowed to live seventeen days after operation. At this time, they were anesthetized with ether and bled to death. The brains were immediately removed from the skull and put through a series of alcohols. Camera lucida drawings were made of the brains showing the extent of the lesion. The brains were preserved in 70 per cent ethyl alcohol for a brief period. They were then fixed and stained according to Ranson's pyridine-silver modification of the Cajal method (11).

Transverse serial sections were made of the brains extending from the plane of the anterior portion of the diencephalon extending to the caudal portion of the cerebrum. Sections were cut ten microns thick and every fifth section

was mounted and examined. Dr. W. H. Waller, formerly of Boston University Medical School, made a detailed examination of the lateral geniculate of three of the animals (Rats 3, 18 and 20).

CHAPTER VI

RESULTS

STUDY II

The number of trials required to reach criterion in the initial learning period varied from 200 to 420 (see Table VI), and do not include criterion trials. The learning curves for three typical animals are shown in Figures 9, 10 and 11. Individual learning curves for the other animals appear in the Appendix B. The curves show a rather rapid initial rise in the percentage of responses to the Sp. The generalization, increase in responses to Sn, occurs somewhat later and does not give as consistent a picture. Only one animal (see Figure 10) reached and maintained 100 per cent conditioned response for any extended period. The lower and more prevalent response rate of 80 per cent is ascribed in part to the effect of the training to the Sn where failure to respond does not result in shock. Just as the effects of training to the Sp are generalized to the Sn, similarly, the effects of exposure to the Sn generalize to the Sp.

The two blind control animals (Group I) failed to show any signs of learning after six hundred trials,or twice the mean number of trials required by all other animals. This is taken as evidence that the problem could not be solved by the

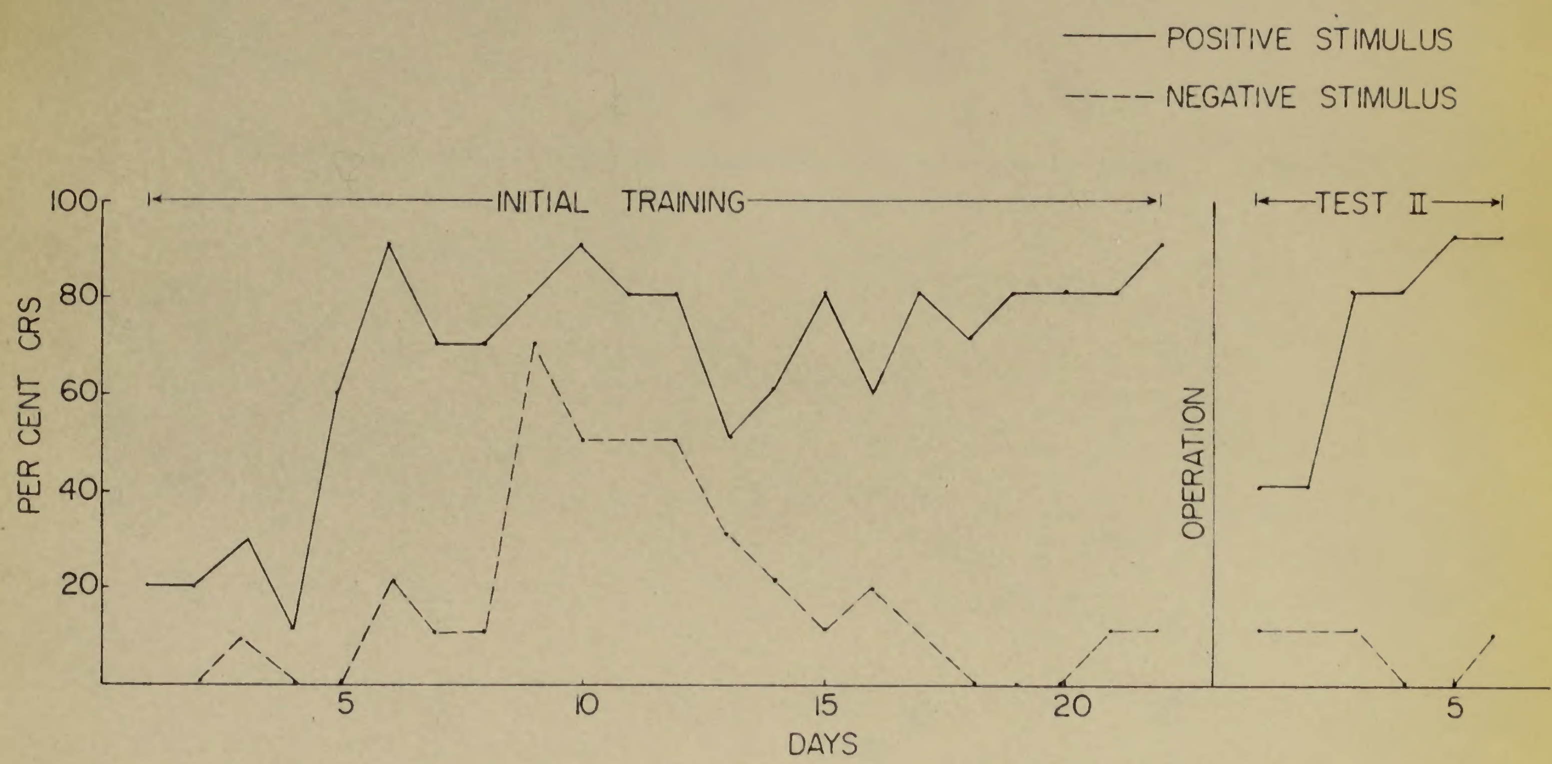

Figure 9

Rat 3. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

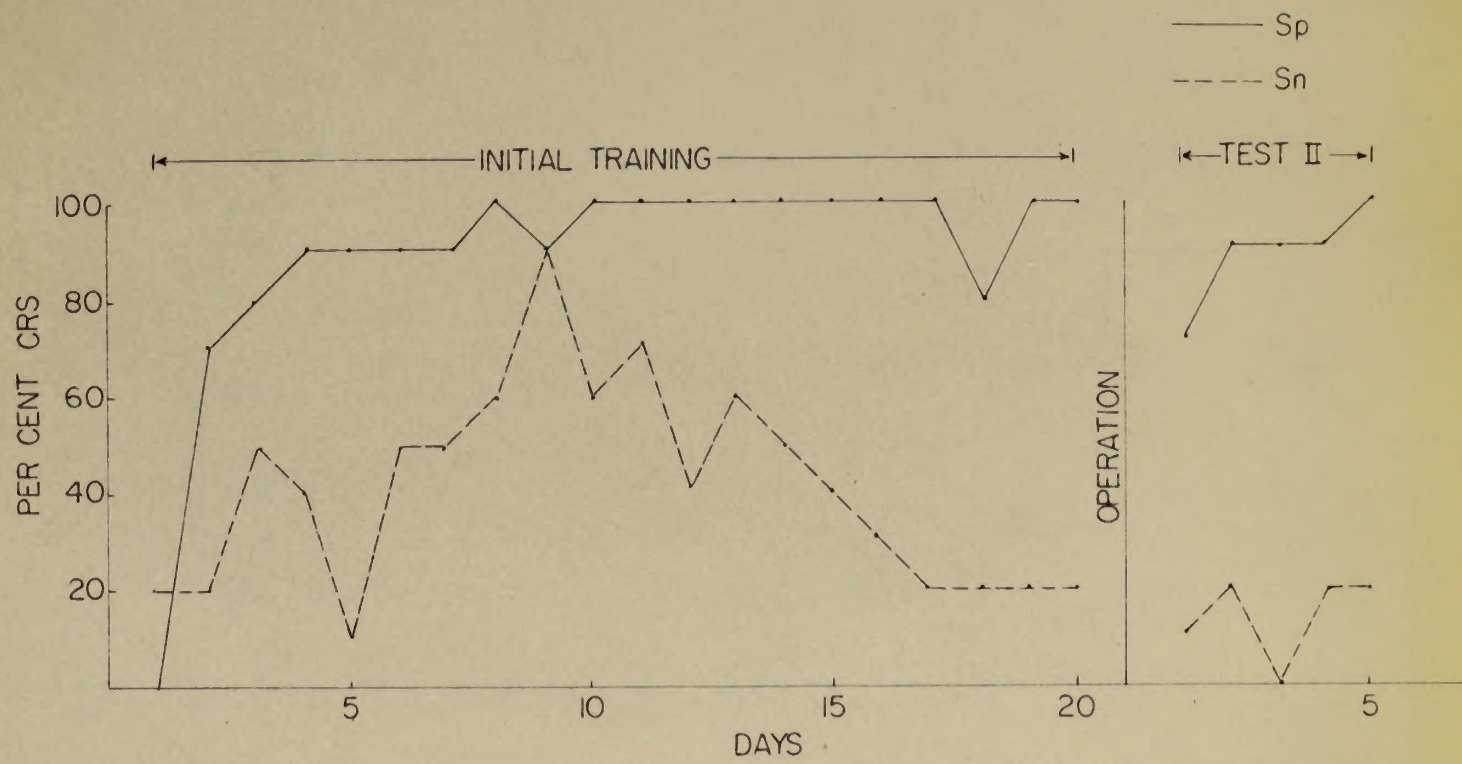

Figure 10.

Rat 9. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

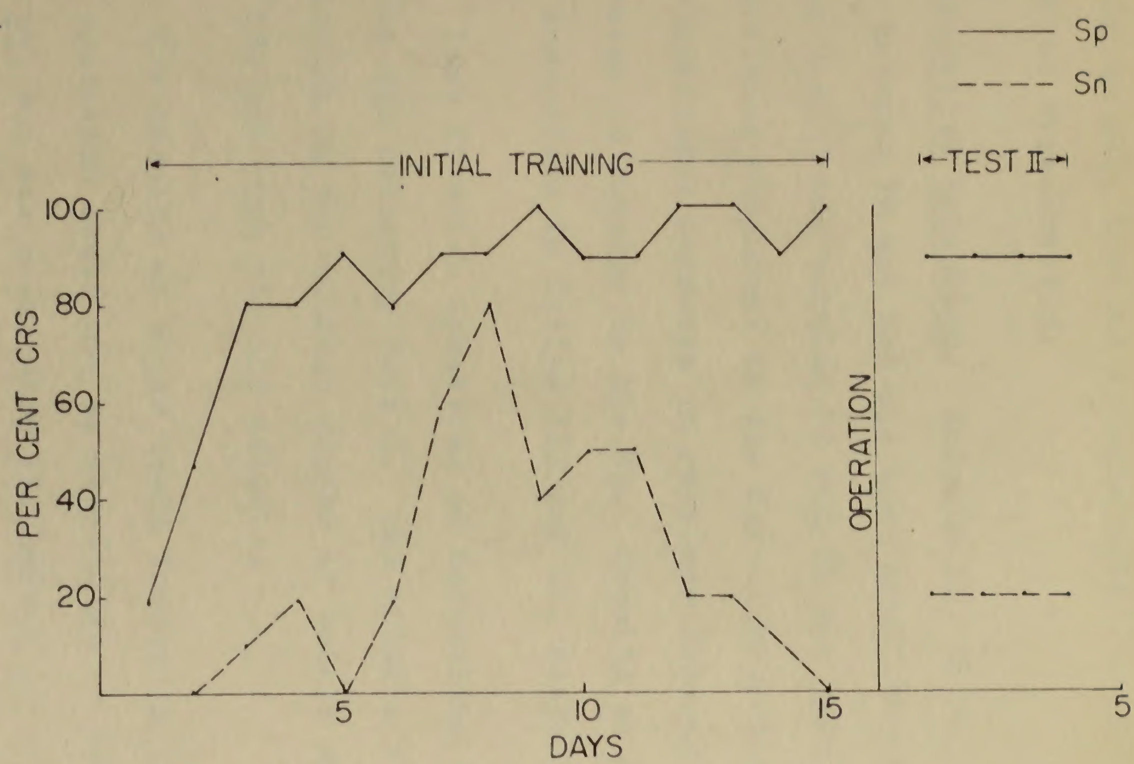

Figure 11

Rat 12. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

use of non-visual cues. The validity of the apparatus as an instrument requiring use of visual cues was further substantiated in earlier studies employing other blind rats and by giving normal, trained animals trials with the conditioned stimulus disconnected.

Preoperative Retention. Animals 17, 18 and 20 (Group III) gave between 70 and 100 per cent conditioned responses to the Sp in Test I and between 10 and 20 per cent generalized conditioned responses to the Sn. A Wilcoxon T Test showed no significant increase in response latency to the Sp or decrease in latency to the Sn. Results of Tests I and II are summarized in Tables III and IV, respectively.

Test II which consisted of retraining trials was started the day following Test I. The animals all reattained criterion in the minimum number of trials such that savings was 100 per cent for all animals.

The results of these tests indicated that any loss following operation could not be attributed to the lapse of time *per se*, but was presumably the effect of operation.

Retention: Control Operation. Rat 22 required 260 trials to reach the learning criterion. In Test I following the control operation the rat made 90 per cent conditioned responses to the Sp and did not make a single generalized conditioned

TABLE III

RETENTION FOLLOWING A FIVE DAY INTERVAL WITHOUT TRAINING AS MEASURED BY TEST I

Rat	Percentage of CRs in Test I		* P of Response Latency Test I	
	Sp	Sn	Sp	Sn
17	80	10	.189	.274
18	70	10	.117	.129
20	100	20	.129	.069

* The response latencies in Test I were compared with the response latencies of the last training session by means of the Wilcoxon T.

TABLE IV

TRIALS TO CRITERION IN INITIAL LEARNING AND RESULTS OF TEST II FOLLOWING A FIVE DAY INTERVAL WITHOUT TRAINING

Rat	Trials to Criterion In Initial Learning *	Number of Trials To Reattain Criterion	Per cent Savings
17	200	0	100
18	200	0	100
20	200	0	100

* The number does not include criterion trials.

response to the Sn. The latency of responses following operation were not significantly greater as determined by the Wilcoxon T ($p > .05$). The results of Test II showed 100 per cent savings. See Tables V and VI and Figure 12.

According to the results of both Test I and Test II, this animal displayed a high degree of retention for the conditioned differentiation. The results are offered as evidence that neither the operative procedure nor the removal of non-striate cortex results in the loss of the learned response. It follows that any loss incurred in the experimental animals is ascribable to lesions to the striate area of the cortex rather than to lesions to the cortex in general.

Total Responses. The total number of responses made by each animal during each session was recorded. A typical curve is shown in Figure 13. The number of responses made during a session ranged from 13 to 120 over a total of 58 sessions,, or 29 days not including the five day postoperative recovery period. A rank correlation for total responses and conditioned responses for each session yielded an r of - .25 for Rat 3 whose responses appear in Figure 13.

If an animal ran continuously during sessions in which the Sp was presented, that animal would achieve a score of 100 per cent conditioned responses as conditioned responses are defined in this study. Responses were evenly distributed

TABLE V

RESULTS OF TEST I GIVEN POSTOPERATIVELY

Group	Rat	CRs and Generalized CRs in Test I		* P of Response Latencies in Test I	
		No. of CRs to Sp	No. of Generalized CRs to Sn	Sp	Sn
II	22	9	0	.23	.106
III	17	1	1	.0001	---
	18	4	2	.0018	---
	20	0	0	.0001	---
IV	9	1	0	.0001	---
	10	8	2	.042	.203
	11	0	1	.0003	---
	12	8	3	.109	.067
	13	8	0	.048	.115
V	2	7	2	.164	---
	3	3	1	.035	---
	5	2	1	.0001	---

* The response latencies of the last preoperative session were compared with the latencies of the first postoperative session by means of the Wilcoxon T. Blanks appear in cases where the animal failed to respond before and after operation to the majority of presentations to the Sn.

TABLE VI

TRAINING TRIALS* TO ATTAIN CRITERION AND RESULTS OF TEST II GIVEN POSTOPERATIVELY

Group	Rat	No. of Trials to Reattain Criterion	No. of Trials to Reattain Criterion Postoperatively	Percentage Savings
II	22	260	0	100
III	17	200	0	100
	18	200	0	100
	20	220	20	90.9
IV	9	320	20	93.8
	10	380	0	100
	11	420	20	95.2
	12	220	0	100
	13	240	0	100
V	2	300	80	73.3
	3	360	40	88.8
	5	240	40	83.3

* The number does not include criterion trials.

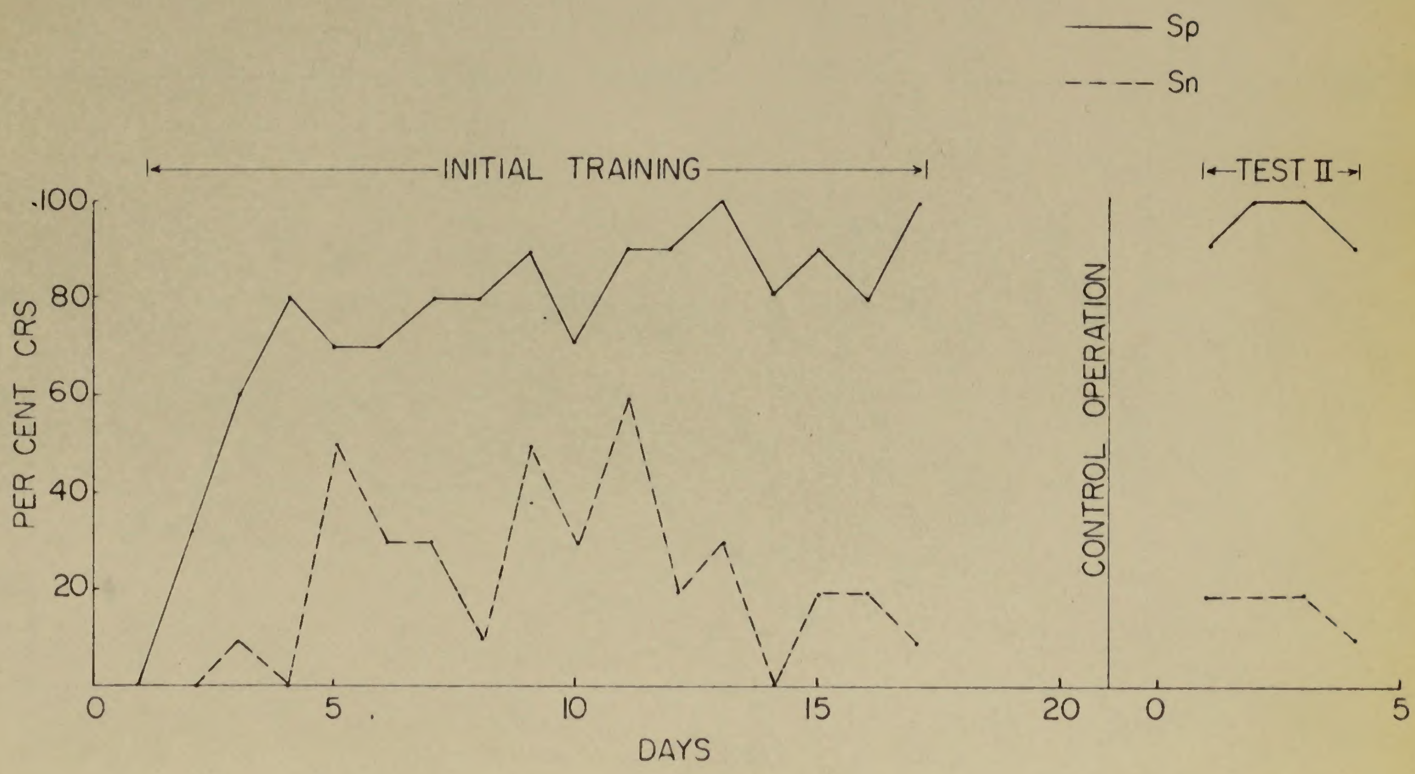

Figure 12

Rat 22. The effect of a control operation on the retention of a conditioned differential response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

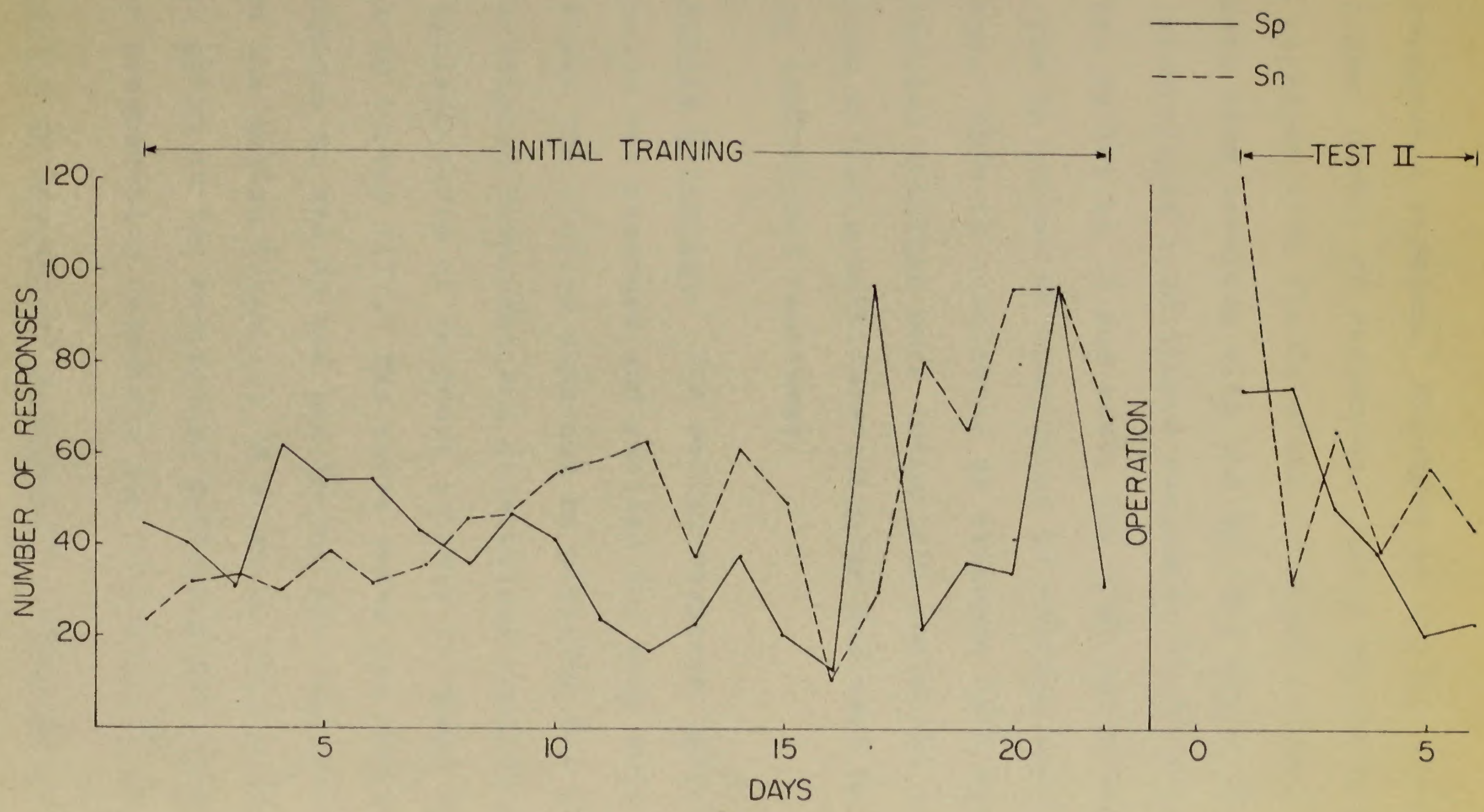

Figure 13

Rat 3. Total number of responses made during sessions with the Sp and the Sn.

throughout a session. Exposure to the Sp did not produce a higher number of responses. Since the number of responses in sessions with the Sn often produced as many or more responses than sessions with the Sp, and since the percentage of generalized conditioned responses in such sessions was often as low as 10 per cent, the high percentage of responses to the Sp cannot be attributed to running behavior (responses) alone. This is considered as evidence that the conditioned responses obtained were intimately connected to the presentation of the conditioned stimulus and were in effect _bona fide_ conditioned responses.

Response Latencies. The median response latency for each session was recorded and plotted for each animal. The curves reflect the picture obtained by plotting the percentage of conditioned responses and generalized conditioned responses. A typical curve of response latency is shown in Figure 14 for Rat 18 (Group III). The curve shows the median latency of response to the Sp and the Sn for the last ten training days and the median latencies in Tests I, II and III. Test I was given on two occasions: following the five day interval for preoperative retention and following surgery.

Results of Operation: Anatomical. Examination of the lateral geniculate, _pars dorsolis_, in Rats 3, 18 and 20 revealed that the cells had completely degenerated. This finding indicates

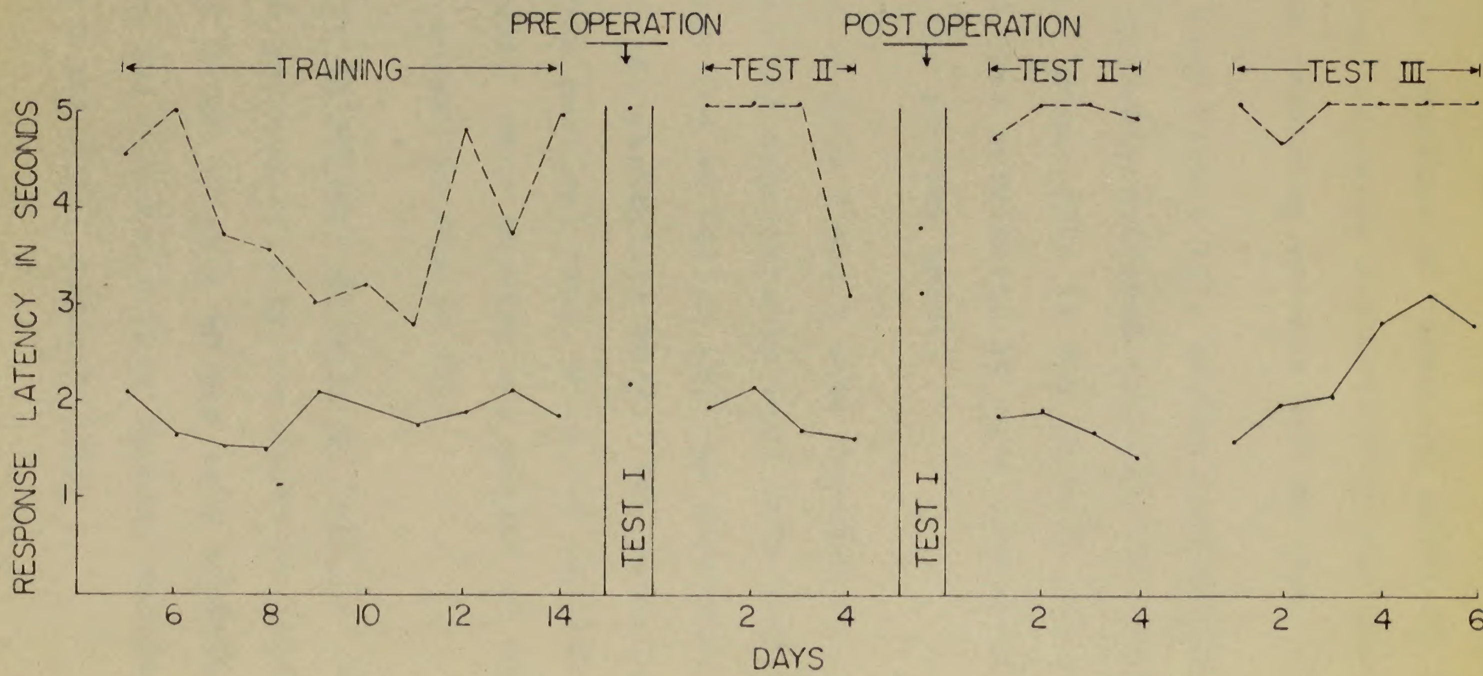

Figure 14

Rat 18. Median response latencies for last ten training days and for Tests I, II and III. Each day the animal was given ten trials to each stimulus.

complete destruction of the striate area of the cortex in these animals. Because of technical problems in staining and sectioning, adequate evaluation of the lateral geniculate bodies in the remaining animals was not possible.

Rat 17 (see Figure 15), having more extensive lesions than Rat 3, probably suffered complete destruction of the striate area. Since this is not certain however, only Rats 3, 18 and 20 were considered to have undergone complete destruction of the striate area.

Lesions in Rats 2 and 9 were incomplete. The cortical area involved was considerably less than that described by either Lashley (6) or Waller (17) as receiving projections from the lateral geniculate body. The remaining animals, as judged from cortical maps, also had partial lesions of varying extent. Maps showing the extent of cortical lesions in the rats appear in Figure 15.

<u>Postoperative Retention</u>: <u>Results of Test I</u>. The results of Test I given postoperatively are shown in Table V. Rats 10, 12 and 13 of Group IV gave 80 per cent conditioned responses to the Sp in the ten extinction trials, whereas Rats 9 and 11 gave 10 and 0 per cent, respectively.

The percentage of responses to the Sn remained uniformly low for all animals.

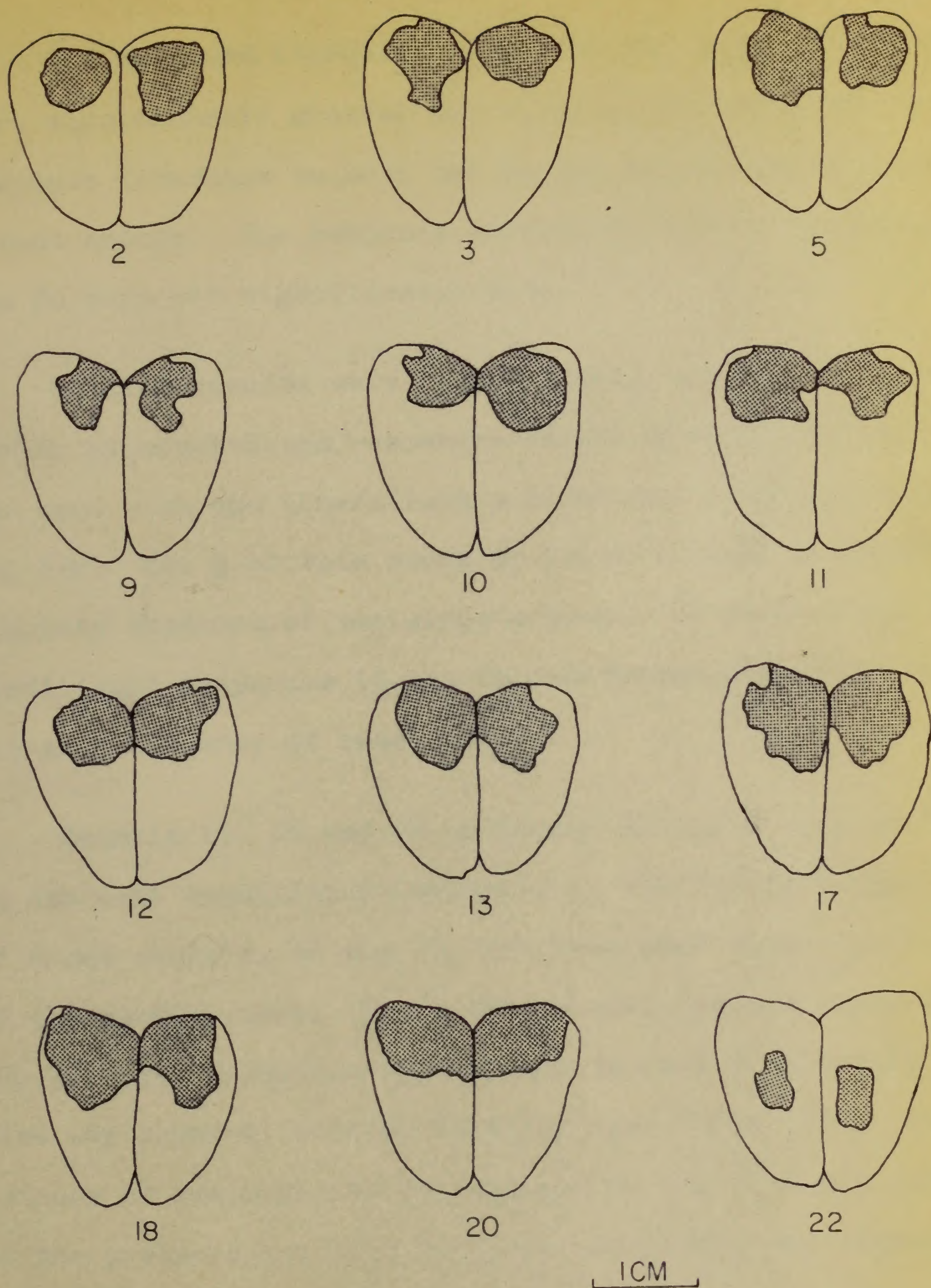

Figure 15

Camera lucida drawings of rats' brains made at necropsy. Hatched areas indicate extent of lesion. The rat may be identified by the number below each drawing.

The response latencies to the Sp for animals in Group IV were significantly greater for allanimals except Rat 12 whose response latencies to both the Sp and the Sn showed no significant change. The response latencies of Rats 10 and 13 to the Sn were not significantly less.

Similar results were found to hold in Group V. The number of conditioned responses varied from 20 per cent to 70 per cent with the generalized conditioned responses remaining low. Rat 3 of this group is known to have undergone complete ablation of the striate area. He gave 30 per cent conditioned responses to the Sp and showed a significant increase in latency of response.

Animals 17, 18 and 20 of Groups III made between 0 and 40 per cent conditioned resposnses in the test series. Two of these animals, 18 and 20, had undergone total ablation of the striate area. These same animals gave between 70 and 100 per cent conditioned responses in Test I following a five day interval without training (see Table III). The latency of response had not changed in the five day interval of the preoperative test but postoperatively the increase in latency was significant beyond the .0018 point for both animals.

All animals with complete lesions gave a low percentage

of conditioned responses to the Sp following operation, and the response latency increased significantly. Animals with partial lesions produced a varied picture giving as few conditioned responses as animals with total ablation in some cases, while in others they gave as many conditioned responses as they had preoperatively.

A sign test revealed no significant difference ($p > .25$) between the number of conditioned responses occuring in the first half of the trials in Test I and the number of conditioned responses in the second half of the trials. It is unlikely, therefore, that the significant differences found in response latencies are a result of the extinction process.

<u>Postoperative Retention: Results of Test II.</u> The day following Test I, which was six days after operation, animals were given the first of a series of retraining trials constituting Test II. The results of the test together with the initial number of trials to attain criterion appear in Table VI.

Retraining was continued until the animal gave 80 per cent conditioned responses or more to the Sp and no more than 20 per cent generalized conditioned responses to the Sn for four consecutive days. The percentage of savings varied from 73.3 per cent to 100 per cent. These savings scores are particularly large in view of the ten extinction trials to the Sp and the ten trials to the Sn given on the previous day.

<u>Group IV and V Compared</u>. The brighter of the two light stimuli served as the Sp for Group IV, whereas the dimmer light served as the Sp for Group V.

Group IV required a mean of 316 trials to reach the learning criterion initially and required a mean of eight trials to reattain criterion after operation. Group V required a mean of 300 trials to attain the initial learning criterion and a mean of 53.3 trials to reattain criterion postoperatively.

A T Test of significance was applied to determine whether the difference for initial learning was larger than might be expected on a chance basis. A second T Test was run to test the significance of the difference in trials to relearn.

The test revealed there was no significant difference in the mean number of trials for initial learning ($p > .10$). The second T yielded a p value of beyond .01. Thus, when considered as a group, animals trained with the dimmer light as the Sp, took longer to reattain criterion than animals trained to the brighter light as the positive stimulus.

<u>Results of Test III</u>. Trials with the shock supply disconnected were given to four animals following the completion of retraining in Test II. Since Test III was not part of the original experimental plan, not all animals were given the

test. The animals included were: Rats 10 and 11 (Group IV) and Rats 17 and 18 (Group III). The results of these trials are shown in Figures 18, 19, 21 and 22.

Conditioned responses to the Sp were completely extinguished in Rats 10 and 11 after thirty and forty extinction trials, respectively. The number of generalized conditioned responses remained about 20 per cent in the same number of trials.

Rats 17 and 18 gave approximately 50 per cent conditioned responses to the Sp after sixty extinction trials. The responses to the Sn in Rat 18 dropped to zero, whereas the number of generalized conditioned responses to the Sn increased to 60 per cent over the sixty trials.

In order to obtain uniform histological results, all animals were sacrificed seventeen days after operation, at which time the brains were removed and fixed in alcohol. For this reason, Test III had to be terminated before complete extinction to the Sp was achieved.

CHAPTER VII

DISCUSSION

The results of Test II confirm the findings of Wing and Smith (21) with respect to retention of a conditioned response to light as measured by the savings method. The dogs in the above study showed from 78 to 100 per cent savings. The rats in the present study demonstrated between 73 and 100 per cent savings.

In the case of Rats 18 and 20, with complete ablation of the striate cortex, preoperative tests showed no increase in response latency over a five day period without training. Following operation, the response latencies increased significantly. A similar increase in response latency occured in the case of Rat 3, another animal with total extirpation of the striate area, though this animal was not given a preoperative test of retention. Hilgard and Marquis (6) also found an increase in response latency following operation in their test of retention of the conditioned eyeblink in dogs. Their animals, however, did not show any change in frequency of conditioned responses. This situation is comparable to that of Rat 10 and 13 where the postoperative percentage of conditioned responses remained at 80 per cent though the response latencies increased significantly.

In studies employing conventional discrimination box

situations (2, 3, 5, 14), rats required as many trials to reattain criterion after operation as originally required. The lowest savings score achieved in the present study by any rat was 73.3 per cent, and is comparable to the savings scores obtained in work with dogs (21). Since the response conditioned in Study II involved gross bodily movement similar to that employed in discrimination studies, loss of the response in the latter, following operation, cannot be accounted for in terms of differences in muscular involvement.

Marquis and Hilgard found that when their dogs were tested for retention of a conditioned eyeblink two days after operation, the animals failed to respond. The dogs were tested again five days after operation, without intervening reinforcements, and gave 100 per cent conditioned responses at this time. The phenomena has been termed diaschisis. There has been no adequate explanation of the effect but it has been observed on a number of occasions. The low percentage of conditioned responses given by most of the rats in Test I of Study II may be the effect of having tested the animals too soon after operation. The cats in Study I were given a period of fourteen days in which to recover from the operation. The percentage of conditioned responses in these animals when first tested was comparatively high.

Contrary to the findings of Wing and Smith (21) the animals with partial lesions to the striate cortex were not resistant to extinction following operation. The tendency for the visual and auditory conditioned response to extinguish is apparent in the performance of Cat 3 and relatively rapid extinction of a visual conditioned response was found to occur in the case of Rats 10 and 11 with partial lesions to the striate cortex.

Wing (19, 20) found two dogs with partial lesions to the striate cortex giving a smaller percentage of conditioned responses on the first extinction trials following operation, than dogs with total extirpation of the striate area. Similar results were found in Study II when responses to the Sp are considered. Rat 18 with complete ablation of the striate cortex gave 40 per cent conditioned responses in the ten extinction trials. Rats 5, 9 and 11 with partial lesions gave from 0 to 20 per cent conditioned responses in a similar number of trials.

A technique developed in conjunction with the present investigation involved the mapping of the visual area of the cortex of the rat by recording potential changes in the cortex following visual stimulation.[1]

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1 The technique, suggested by Professor J. M. Harrison, was investigated at the Boston University Experimental Psychology Laboratory for several months and the visual area of a number of rat brains was mapped.

The results obtained by physiologists in studies with cats and monkeys using a similar method have differed from the results obtained by anatomical procedures (14, 22).

A portion of the cortex adjacent to the striate area showing potential changes following stimulation has been termed, Visual II. At the present time, no functional maps of the rats' visual area are available.

Since little research has been done based on Visual II, and since the reliability of the recording apparatus and technique used in this study was not established, it was thought advisable to follow maps based on anatomical data.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

The present study was undertaken (a) to determine the effect of partial and total extirpation of the striate area of the cortex on the retention of a conditioned differentiation of two light stimuli; (b) to investigate the effect of partial lesions to the striate cortex on previously acquired conditioned responses; (c) to determine whether or not findings based on research with dogs and monkeys apply to animals lower on the phylogenetic scale; (d) to learn whether or not lesions to the striate area of the cortex produce the same effect on the retention of previously learned gross bodily responses as are produced on segmental responses acquired in a conditioning situation.

In Study I four cats were trained in a conditioned avoidance situation to a visual and to an auditory stimulus with electric shock serving as the unconditioned stimulus. To avoid shock the cats were required to respond within 2.8 seconds of the onset of the conditioned stimulus (light or sound).

Upon achieving criterion the animals were given a rest period of approximately two months during which time they continued with normal cage living. At the end of the period,

they were tested for retention of the response.

Following several sessions introduced to restore the response level, the cats underwent subtotal occipital lobectomy in which portions of the striate cortex were removed. After a fourteen day recovery period the animals were tested for retention of the conditioned response. Varying amounts of extinction and reconditioning were given. The animals were then killed and their brains removed and examined.

Study II employed 24 male, albino rats as subjects. The animals were trained to respond differentially to two light stimuli differing in intensity.

The rats learned to avoid electric shock by running to a different sector of the apparatus in which they were trained within 2.5 seconds of the onset of the positive light stimulus (Sp). The response to the Sp generalized to a second light stimulus (Sn) which was never followed by shock.

Training was continued until the animal made 80 per cent conditioned responses or more to the Sp and no more than 20 per cent generalized conditioned responses to the Sn for four consecutive days.

Upon achieving criterion the striate area of the cortex was removed and five days later the animals were tested for

retention of the conditioned differentiation.

Two tests of retention were given. The first consisted of ten trials to each stimulus with the shock circuit disconnected. The second test consisted of retraining until the animal again achieved criterion, thus yielding a savings score. Following these tests, four animals were given a series of extinction trials.

A number of control animals were used to insure that (a) the task set for the animals could not be solved by use of non-visual cues; (b) loss, should it occur, could not be attributed to the trauma associated with the operation; (c) the task would be retained by normal animals over a period of time comparable to the recovery period following operation.

Seventeen days following operation, the animals were killed; the brains were removed from the skull and fixed in alcohol. Portions of the brain including the lateral geniculate bodies were then stained, mounted and examined.

The results of the two studies lead to the following conclusions: (a) Animals undergoing complete extirpation of the striate area of the cortex following acquisition of a differential conditioned response to two light stimuli differing in intensity retain that differentiation postoperatively when retention is measured by the savings

method. Animals with partial lesions give similar results. (b) Both cats and rats undergoing partial lesions to the striate area following acquisition of a conditioned response to light retain that response postoperatively. (c) Survival of a conditioned response to a visual intensive stimulus following complete ablation of the striate area is not restricted to dogs and monkeys but applies also to rats. (d) Postoperative retention of a conditioned response to light is not restricted to behavior involving segmental responses. Rats with complete extirpation of the striate area, and both cats and rats with incomplete extirpation of the striate cortex, retain a conditioned response postoperatively when the response involves gross bodily movement. (e) The latency of conditioned responses to light as measured in extinction trials was found to increase in all but two rats following lesions to the striate area of the cortex. The response latencies returned to their preoperative level after few reinforcements. (f) Cortical lesions involving the projection area of the lateral anterior nucleus has no effect on the retention of a conditioned differentiation of two light stimuli. (g) Conditioned avoidance responses to light stimuli are not particularly resistant to extinction following partial lesions to the striate area.

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APPENDIX A.

PRELIMINARY STUDIES

PRELIMINARY STUDIES

The investigation reported in Studies I and II initially started as an attempt to discover why learning measured in a conventional conditioned response framework survived removal of the visual cortex, while learning measured as a discrimination does not survive the operation. Exploratory experimentation in the area revealed that the problem would require years of research and extended beyond the scope of the experimentation contemplated. Accordingly, a restricted aspect of the broader problem was selected and is described in Chapter I.

Exploratory work for Study I involved an attempt to train cats to perform a conditioned avoidance response such as used by Wing (19, 20) with dogs. Several months of training with four cats involving numerous variations in apparatus and procedure failed to accomplish the desired results. The attempt was abandoned.

A training box was build and successive modifications were introduced until the animals succeeded in producing the behavior desired by the experimenter. Approximately three hundred trials were required to bring the animals to a steady level of responding to the conditioned light stimulus.

The final procedure and apparatus adopted are given in detail in Study I.

On completing the study with cats, it was decided to continue the experimentation with rats using a modified model of the same training apparatus.

Cats proved to be much more difficult to maintain than rats. They also proved to be more susceptible to disease than rats kept under approximately the same living conditions. Four cats died of pan-leucopenia soon after arriving at the laboratory, and it then became standard procedure to vaccinate the cats on arrival. Eye infections developed in a number of animals. They were treated by washing the eyes with a dilute solution of boric acid.

The excessive heat in the laboratory during summer months rendered the animals unfit for training and operation at this time was judged unwise.

These problems together with difficulties in training and equally difficult problems in operation, led to the abandonment of cats as subjects. The larger brain of the cat was a small advantage compared to the many disadvantages in their care and training.

<u>Experimental</u> <u>Methods</u>. A box was build (18 inches by 3 inches by 3 inches) and substituted for the training box used in

the cat study. The shock supply was reduced to 400 volts D. C. with fixed resistance in series to deliver approximately 1.1 milliamperes of current through the animal when he stood on alternate grids of the floor. The spring tension holding the box in place was reduced making the box more sensitive to movement of the animal, and hence lowered the force required to close the switches. The animals were given thirty trials per day for five days.

The subjects consisted of four male, albino rats, previously trained and extinguished on the Gagne maze. The animals were approximately four months old.

The animals failed to learn the appropriate response. A great deal of struggling occured in the initial trials but the activity failed to close the switches. During the last training sessions the animals remained motionless.

Several modifications were introduced in the apparatus and procedure but all attempts resulted in failure. The apparatus was discarded.

Shock Intensity. The first investigation using the circular grid, finally adopted and described in Study II, revealed that a shock intensity of 1.1 milliamperes was too high for optimum learning. Approximately one half of the animals failed to move after the onset of shock. These animals remained immobile during the entire training session. Later

reduction of shock intensity to .8 milliamperes failed to restore the level of the running response existing before the initial shock.

<u>Training Procedure</u>. The rats were given ten trials per day to the Sp until they reached a criterion of 80 per cent conditioned responses for two consecutive days. At the end of this period five trials per day were given to the Sp and five trials to the Sn with the two stimuli randomly distributed throughout the ten trials.

The slow rate of learning suggested the number of daily trials be increased. Since the animals had received several days training to the Sp initially it was thought desirable to introduce a number of trials to the Sn in order to equate the number of trials to each stimulus.

<u>Anesthetic and Operative Technique</u>. When training was completed the animals were used to investigate anesthetic problems. A number of anesthetics were tried including Dial (Ciba), Nembutal (Abott) and Nembusen (Abott). The latter proved most satisfactory. A dose of 50 mg. per kg. body weight given interperitoneally to a young rat provided a deep anesthetic lasting a full hour or more. The dose was given in a single injection and maintaining doses were not needed. Rarely did the anesthetic fail to take effect nor

did serious breathing difficulties arise as was often found in cases where ether was used as a supplement.

The operative technique finally adopted went through a large number of stages and was developed over a considerable length of time. All laboratory animals when discarded after completing training were operated and the lesion subsequently examined.

The procedure for removing the brain from the skull followed that described by McClung (11) though the technique was developed independently.

Younger animals, having thinner skulls, and responding more uniformly to anesthesia were preferable as subjects from an operative point of view.

The findings thus far reported were incorporated in the following investigation.

Subjects and Procedure. This study involved use of eighteen young, naive, male, albino rats. They were given standard preliminary training. The trials of the first training schedule consisted of twenty trials per day to the Sp. The inter-trial intervals were 30, 45 and 60 seconds presented in random order. The CS-US interval was 2.8 seconds. Other procedural details followed that described in Study II.

After achieving a criterion of 80 per cent conditioned responses to the Sp, training under Schedule II was started. Under this schedule, the animals received five trials to the Sp and fifteen trials to the Sn for as many days as originally required to reach criterion under Schedule I. The trials to the Sp were introduced randomly throughout the series of trials to the Sn.

When the appropriate number of trials had been given, the animals were put on a third training schedule. They were given twenty trials per day, ten trials to each of the two stimuli distributed randomly throughout the series.

Following preliminary training, two of the animals in the group were blinded by eneculation of the eyes, and trained under Schedule I, that is, they received twenty trials per day to the positive stimulus only. The rats failed to meet criterion of Schedule I after 280 trials. Criterion consisted of 80 per cent conditioned responses to the Sp and a maximum of 20 per cent generalized conditioned responses to the Sn for four consecutive days. At least eighty additional trials would have been required to achieve criterion.

The results of the study led to the introduction of two changes in procedure. The duration of a trial was changed from twelve seconds to five seconds. Observation of latencies

indicated that if the animals failed to respond after five seconds of exposure to shock there was little likelihood that the subject would move if the shock circuit remained closed for a longer period.

The slow rate of learning was attributed largely to the short interval between shock and non-shock trials. The failture to achieve criterion came in the high response rate to the Sn rather than failure to respond to the Sp.

The degree of generalization could have been reduced by lowering the intensity of shock to the Sp. Such a procedure however, would have increased the time required to learn the conditioned response to the Sp. Increasing the difference between the intensities of the light stimuli might have resulted in faster differentiation but lowering the intensity of the Sn ran the danger of bringing the intensity below postoperative threshhold. Increasing the intensity of the Sp involved danger of introducing non-visual cues such as heat or filament noise of the light source.

Consideration of these and other alternatives led to a change in the order of stimulus presentation. The Sp was given in blocks of ten trials followed five hours later by a block of ten trials to the Sn. Each day the order of stimulus presentation was reversed.

A major breakdown in the timing apparatus on the fifteenth day of training casued the experiment to be discontinued.

A new electronic device and shock supply designed and constructed by J. M. Harrison and C. E. Mayer was used. The apparatus contained a thousand volt shock supply. Where .8 milliamperes of current proved an adequate level of shock when a 400 volt shock supply was use, the current intensity with the new voltage supply had to be reduced to .4 milliamperes.

The findings reported in this Appendix were incorporated in Studies I and II.

APPENDIX B.

SUPPLEMENTARY FIGURES

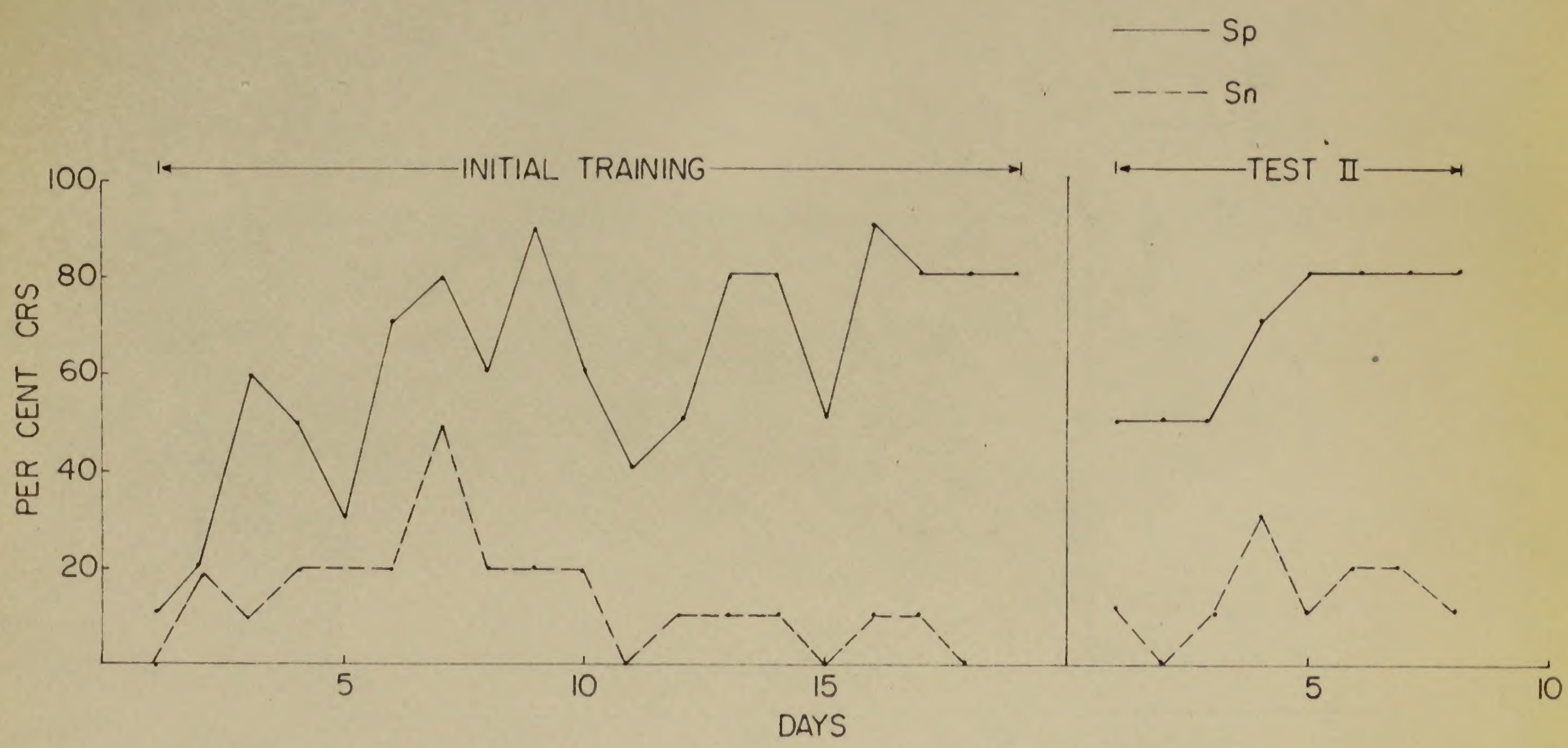

Figure 16

Rat 2. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

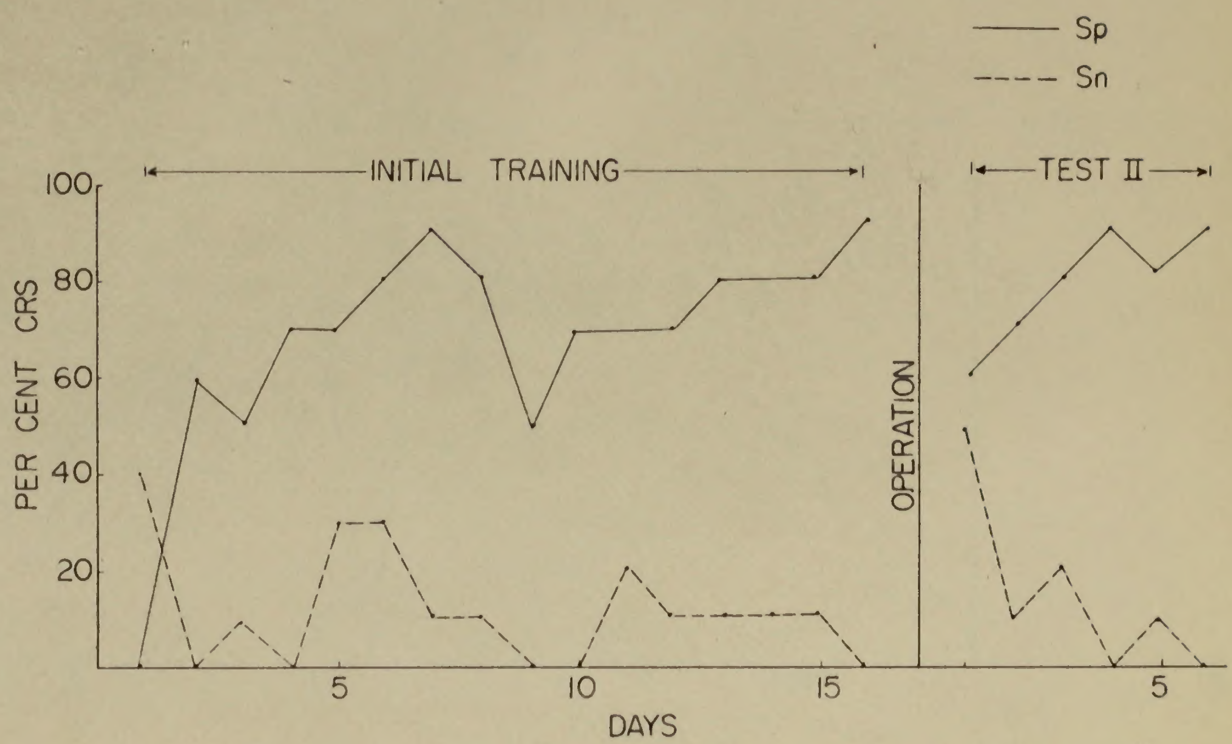

Figure 17

Rat 5. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

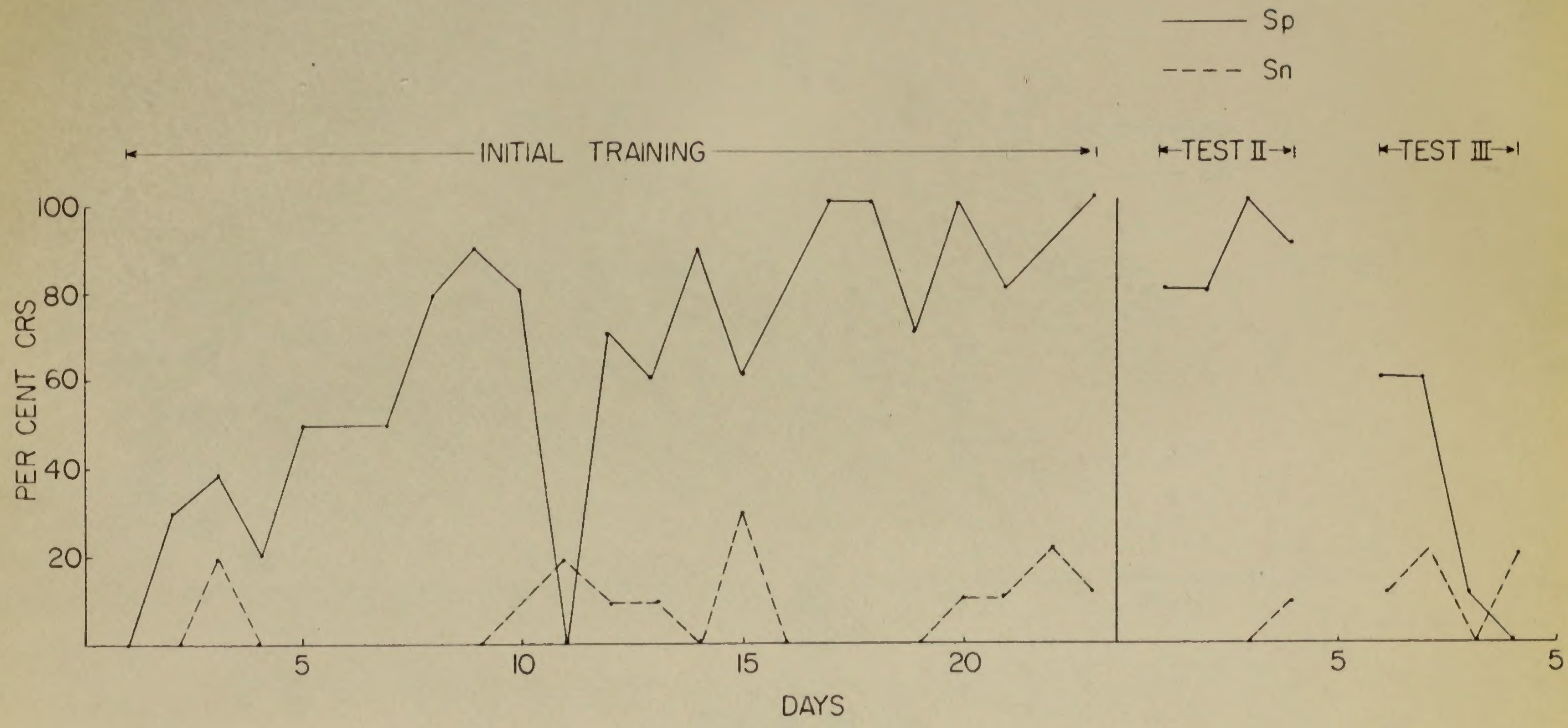

Figure 18

Rat 10. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Test II was started six days after operation. Test III was started two days later.

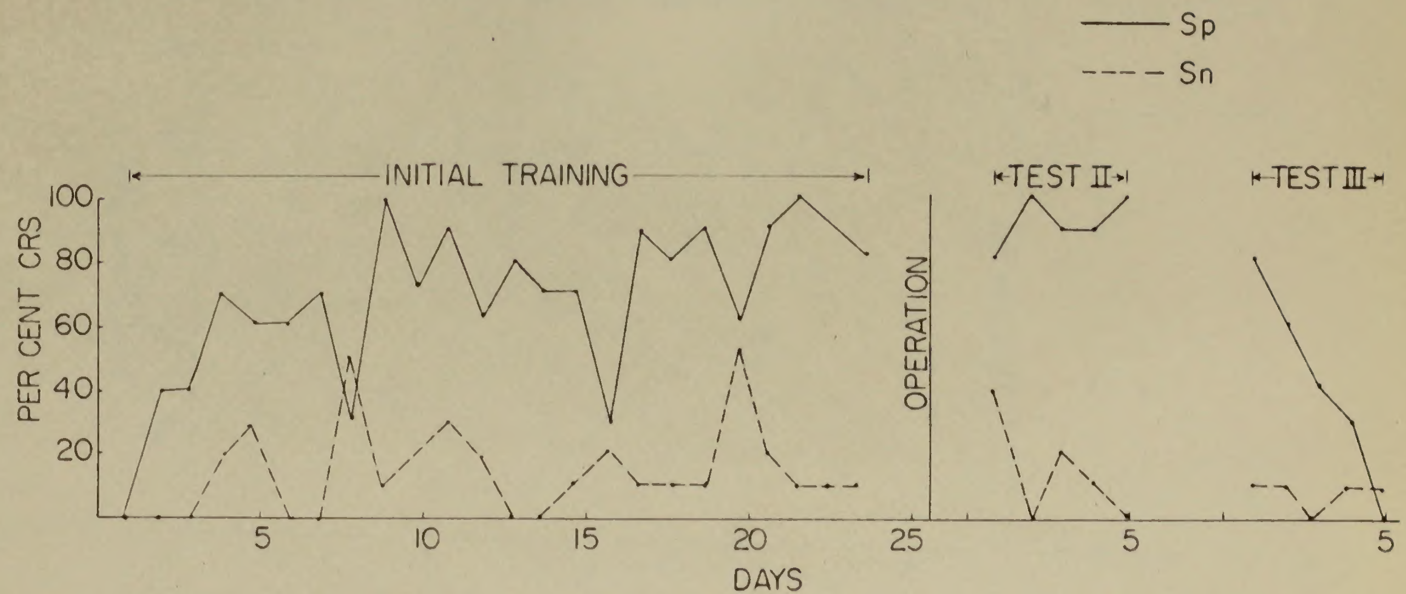

Figure 19

Rat 11. The effect of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials a day to each stimulus. Test II was started six days after operation. Test III was started the following day.

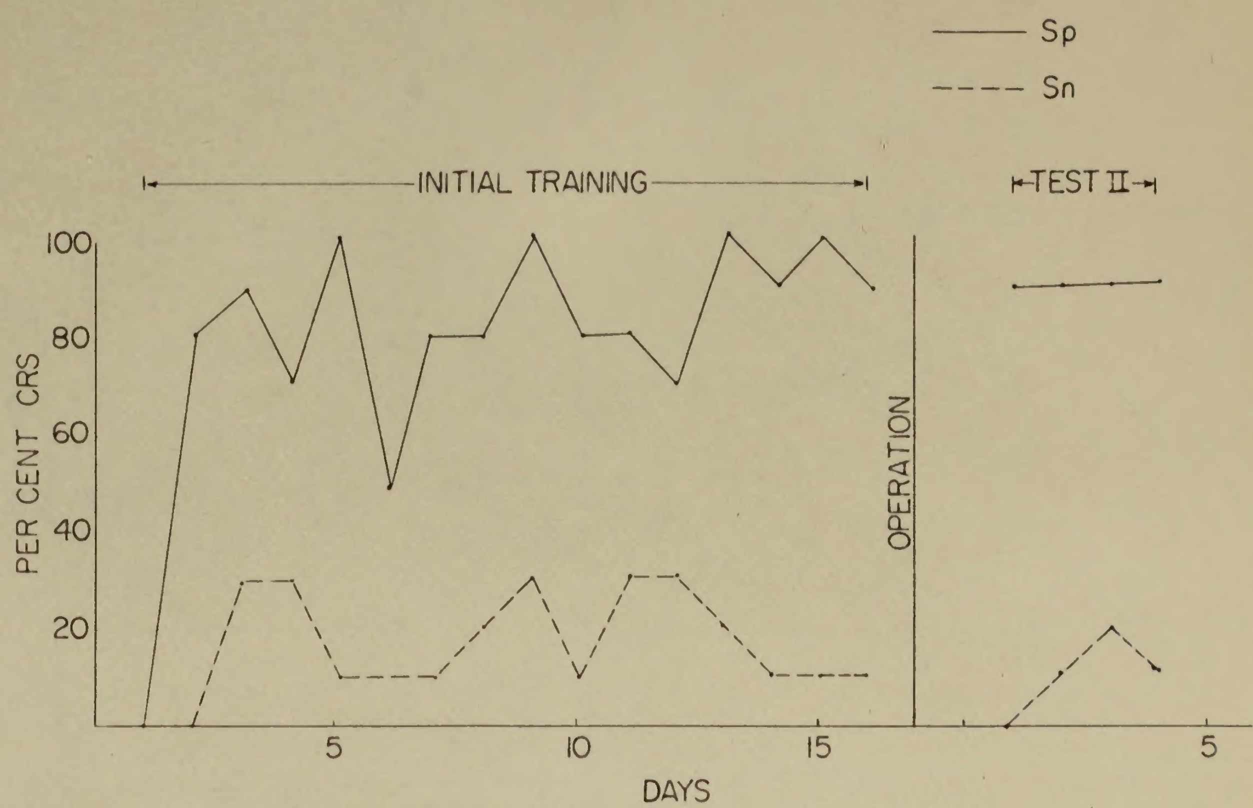

Figure 20

Rat 13. The effects of lesions to the striate cortex on the retention of a differential conditioned response. The animal was given ten trials per day to each stimulus. Retraining (Test II) was started six days after operation.

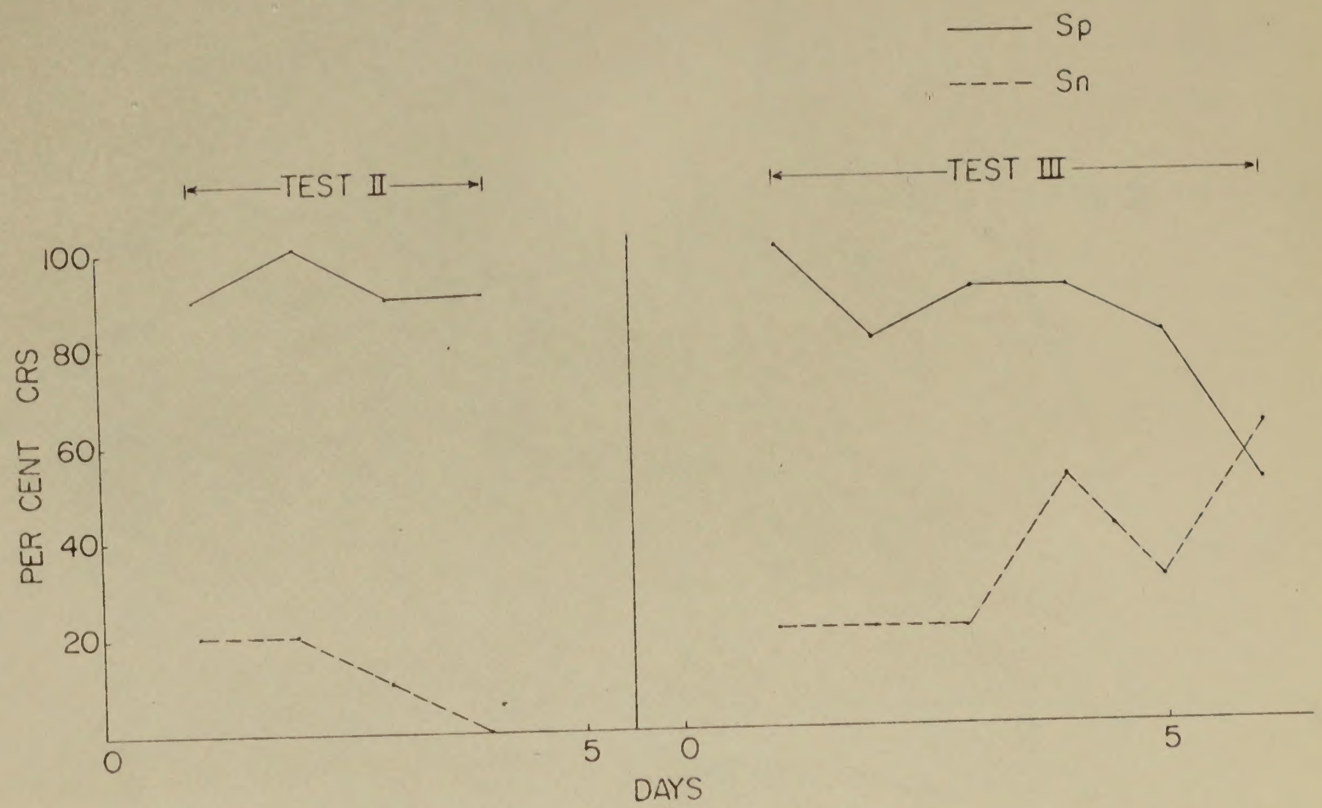

Figure 21

Rat 17. Retraining and extinction following operation. Test II was started six days after operation. Test III was started ten days after operation. Each day the animal received ten trials to each stimulus.

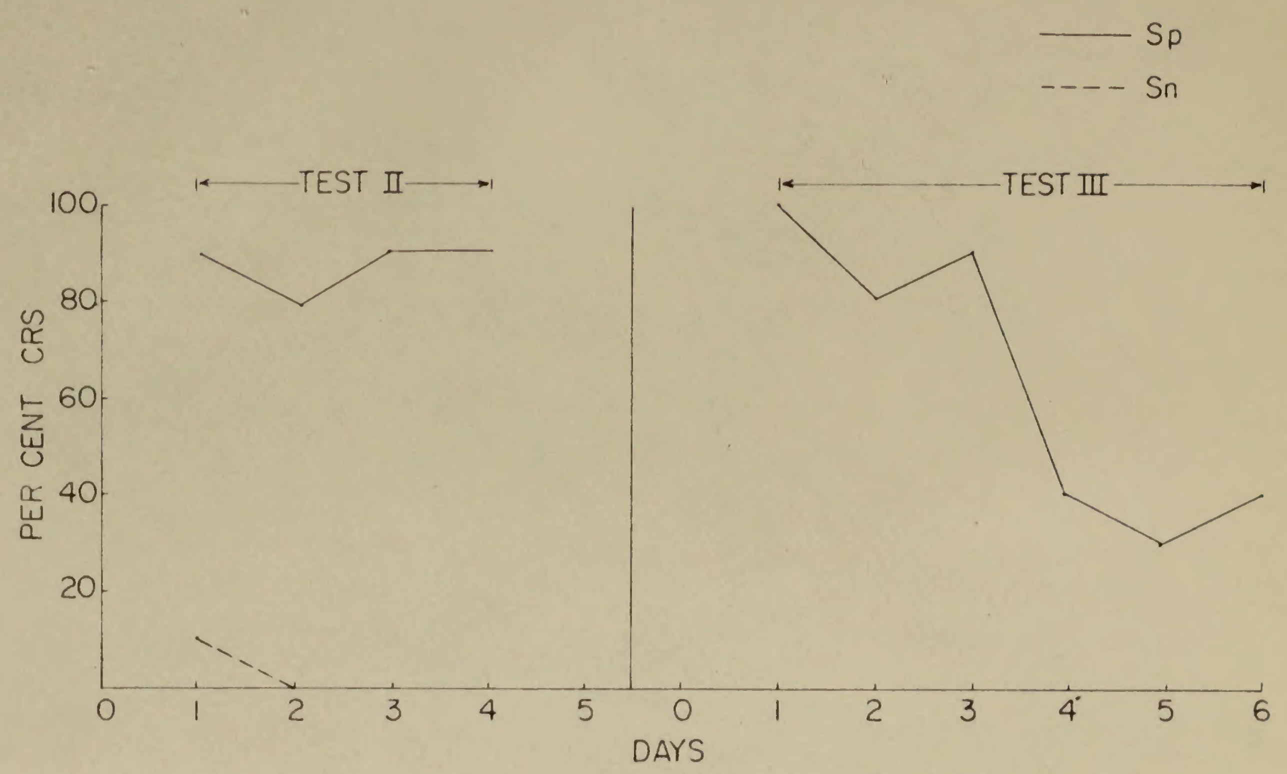

Figure 22

Rat 18. Retraining and extinction following operation. Test II was started six days after operation. Test III was started ten days after operation. Each day the animal received ten trials to each stimulus.

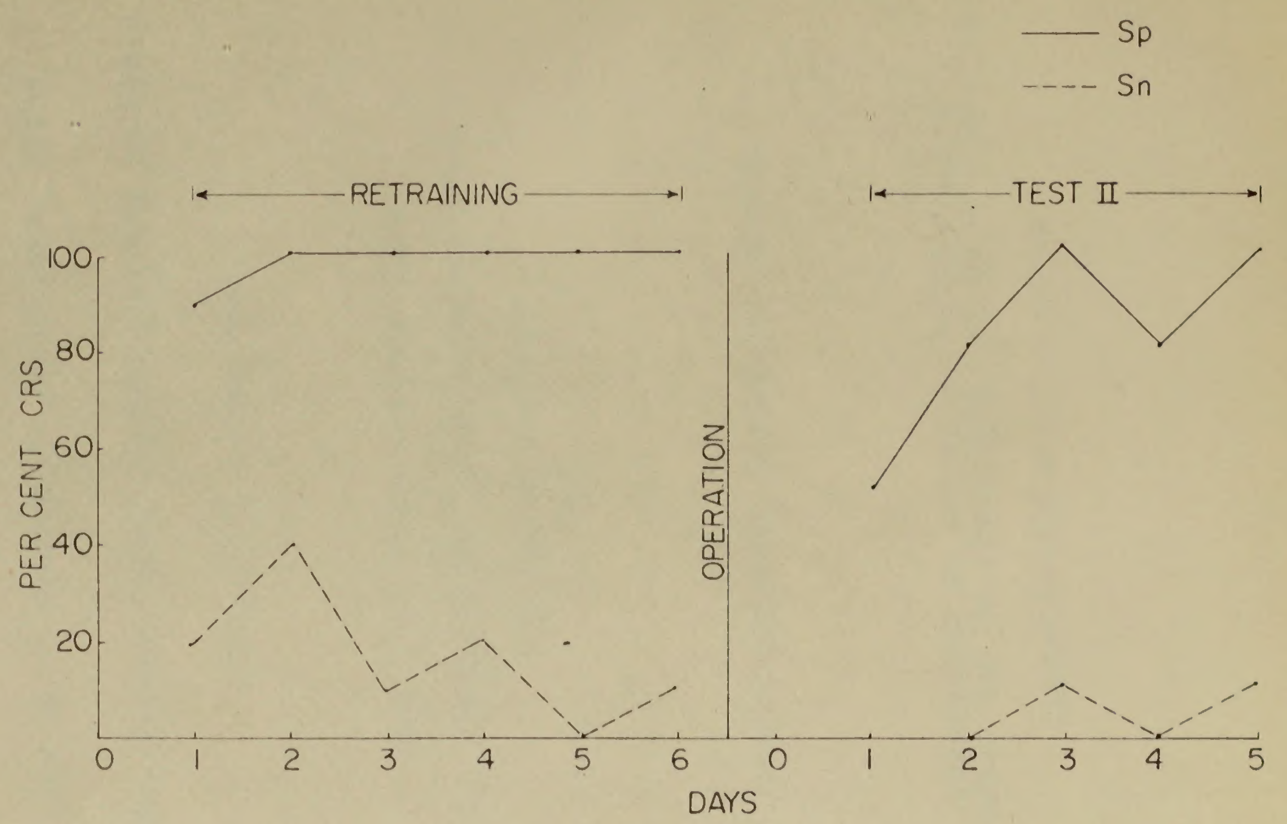

Figure 23

Rat 20. The effect of lesions to the striate cortex on the retention of a differential conditioned response. Retraining followed a fourteen day waiting period. Test II was started six days after operation.

RETENTION OF CONDITIONED RESPONSES TO LIGHT FOLLOWING LESIONS TO THE STRIATE CORTEX

Abstract of a Dissertation

Submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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It is generally agreed that an animal conditioned to a visual intensive stimulus retains that response, at least to some degree, after ablation of the striate area. The conclusion is based on studies that have been restricted in several respects. First, the responses conditioned have been limited to the eyeblink and leg flexion. Second, the experiments have been carried out only on monkeys and dogs. Furthermore, the research in this area, with the exception of an experiment by Wing in which he measured the post-operative retention of a response to direction of light change, has been restricted to use of a single light stimulus. From the available data it is impossible to determine whether a differential response to two stimuli would survive removal of the striate area when the responses are acquired in a conditioning situation.

The present study was undertaken (1) to determine the effect of partial and total extirpation of the striate area of the cortex on the retention of a conditioned differentiation of two light stimuli; (2) to investigate the effect of partial lesions to the striate cortex on previously acquired conditioned response; (3) to determine whether or not findings based on research with dogs and monkeys apply to animals lower on the phylogenetic scale; and (4) to learn whether or not lesions to the striate area of the cortex produce the same effect on the retention

of previously learned gross bodily responses as are produced on segmental responses acquired in a conditioning situation.

Two studies were carried out in order to investigate these problems. The first study employed cats as subjects and the second study used rats.

In Study I, four adult male cats were trained in a conditioned avoidance situation. A light served as the conditioned stimulus and electric shock as the unconditioned stimulus.

The CS-US interval was 2.8 seconds. Responses occuring within this interval resulted in shock avoidance and were termed conditioned avoidance responses. The response latency was recorded by the experimenter.

Each day, the animals were given thirty trials in the apparatus, and when the percentage of conditioned responses to the light stimulus had reached a comparatively high and stable level a second conditioned stimulus, a buzzer, was introduced. Training was continued to the two stimuli, presented in random order, until the animals had received a minimum of three hundred trials (15 trials to each stimulus per day) with a variation of less than four conditioned responses in the daily score to either stimulus for six consecutive days.

After achieving criterion the animals were allowed a "forgetting" period which varied from 53 to 61 days. At the end of this period the cats were given a retention test. The test consisted of fifteen trials with the shock circuit disconnected, and with the stimuli again presented randomly. Following the test, the animals were given several days additional training to restabilize the response.

When retraining was complete the cats were brought to surgery. Lesions were made in the marginal gyrus and parts of the suprasylvian gyrus. The cortical area removed or destroyed corresponded approximately to the area described by anatomists as containing the projections of the lateral geniculate bodies.

Following a fourteen day recovery period, the animals were tested for retention using the procedure employed preoperatively.

At necropsy the brains were examined and drawings of the lesions made with the aid of a camera lucida.

The second experiment (Study II) was performed specifically to determine whether or not an animal conditioned to respond differentially to two light stimuli would retain that response when tested following lesions to the striate cortex.

The training apparatus consisted of a circular grid runway 88 inches in circumference enclosed in acetate walls and divided electrically into six sectors. Switches were so connected as to allow the experimenter to energize any of the six grid sectors of the apparatus.

The subjects consisted of twenty-four, naive, male albino rats, appraoximately ninety days old at the beginning of the experiment.

The animals were given ten trials per day to each stimulus. When presented with the positive stimulus (Sp) the animal could avoid shock by going to a different sector within 2.5 seconds in which event the animal was credited with a conditioned response. If the animal failed to leave the sector on which he was located at the onset of the positive stimulus within 2.5 seconds, he received approximately .4 milliamperes of current delivered through his feet as he stood on alternate grids of the floor. He could escape the shock by going to a different sector. Movement from one sector at any time during training was termed a response. If the animal failed to respond within five seconds, the stimulus went off automatically and the shock circuit was opened and reset automatically for the next trial. The light stimulus was turned off the moment the animal responded. The latency of the response was recorded.

Training to the negative stimulus (Sn) followed essentially the same procedure used in training to the positive stimulus except that in no case was the animal shocked following the onset of the negative stimulus. Response within 2.5 seconds of the onset of the negative stimulus was considered an error and termed a generalized conditioned response.

Animals received training to the two stimuli in blocks of ten trials. The blocks or sessions were separated by a five hour period in a given day. The order of presentation was reversed from day to day.

The learning criterion consisted of 80 per cent conditioned responses or more to the Sp and no more than 20 per cent generalized conditioned responses to the Sn.

Upon achieving criterion the rats underwent extirpation of the striate area of the cortex. Following a five day recovery period, they were given ten trials to the Sp and ten trials to the Sn with the shock supply also disconnected. On the following day, retraining trials were started and continued until the animals again achieved criterion. After reattaining criterion, four of the animals were given a series of extinction trials.

A number of control animals were used to insure that (1) the task set for the animals could not be solved by use

of non-visual cues; (2) loss, should it occur, could not be attributed to the trauma associated with the operation; (3) the task would be retained by normal animals over a period of time comparable to the recovery period following operation.

Seventeen days after operation, the animals were anesthetized with ether and bled to death. The brains were removed from the skulls and fixed. They were stained by Ranson's pyridine-silver modification of the Cajal method.

The following results were obtained:

Two cats with partial lesions to the striate cortex gave approximately 100 per cent conditioned responses to both the visual and auditory stimulus in the first half of the test session following operation. The responses showed no significant increase in latency. ($p > .05$), as determined by the Mann-Whitney U Test. A third cat gave similar results with respect to the auditory stimulus but failed to respond to the visual stimulus on one half of the trials. A fourth cat died before he could be tested.

Three of the rats underwent complete extirpation of the striate area. These animals gave between 0 and 40 per cent conditioned responses to the Sp in a series of ten extinction trials following operation. The percentage of responses to the Sn remained low.

The remaining animals with partial lesions gave from

0 to 80 per cent conditioned responses in the extinction test to the Sp. The percentage of generalized conditioned responses to the Sn remained low in all cases.

The response latencies, for all but two animals, in the extinction test to the Sp were significantly greater ($p < .05$) than in the last preoperative session as determined by the Wilcoxon T.

Savings scores were calculated by dividing the difference between the number of initial and postoperative trials to criterion by the number of trials initially required. The amount of savings varied from 73.3 to 100 per cent.

The results of the two studies lead to the following conclusions: (1) Animals undergoing complete extirpation of the striate area of the cortex following acquisition of a differential conditioned response to two light stimuli differing intensity retain that differentiation postoperatively when retention is measured by the savings method. Animals with partial lesions give similar results; (2) Both cats and rats undergoing partial lesions to the striate area following acquisition of a conditioned response to light retain that response postoperatively; (3) Survival of a conditioned response to a visual intensive stimulus following complete ablation of the striate area is not restricted to dogs and monkeys but applies also to rats; (4) Postoperative

retention of a conditioned response to light is not restricted to behavior involving segmental responses. Rats with complete extirpation of the striate area, and both cats and rats with incomplete extirpation of the striate cortex retain a conditioned response postoperatively when the response involves gross bodily movement; (5) The latency of conditioned responses to light as measured in extinction trials was found to increase in all but two rats following lesions to the striate area of the cortex. The response latencies returned to their preoperative level after few reinforcements; (6) Cortical lesions involving the projection area of the lateral anterior nucleus has no effect on the retention of a conditioned differentiation of two light stimuli; (7) Conditioned avoidance responses to light stimuli are not particularly resistant to extinction following partial lesions to the striate area.

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